Lee A. Dyer
Matthew L. Forister
Editors

The Lives of Lepidopterists

Springer

The Lives of Lepidopterists

Lee A. Dyer • Matthew L. Forister
Editors

The Lives of Lepidopterists

Springer

Editors
Lee A. Dyer
Department of Biology
University of Nevada, Reno
Reno
Nevada
USA

Matthew L. Forister
Department of Biology
University of Nevada, Reno
Reno
Nevada
USA

ISBN 978-3-319-20456-7 ISBN 978-3-319-20457-4 (eBook)
DOI 10.1007/978-3-319-20457-4

Library of Congress Control Number: 2015950346

Springer Cham Heidelberg New York Dordrecht London

Printed on acid-free paper

Springer International Publishing AG Switzerland is part of Springer Science+Business Media (www.springer.com)

Preface

This book is a collection of anecdotes and observations and philosophies by a subset of the scientific community: lepidopterists. Many of the authors in this book do not refer to themselves as lepidopterists, rather they might be ecologists or molecular biologists or systematists, but they all share one thing in common. They all made the decision to spend their lives thinking about caterpillars, and moths and butterflies, which is an odd thing if you pause to reflect. Among people who make their living as scientists, many or maybe most would like to directly improve the fate of humanity by curing disease or inventing an unlimited energy supply.

Lepidopterists are a different folk, because butterflies and moths are not going to save the world. They are beautiful and strange, and the benefit they offer to humanity is more subtle than an everlasting cell phone battery. So why do we do it? An easy answer is because they are really handy study organisms for all kinds of basic questions about how the natural world works, at least in part because they are easily observed. This is particularly true of the butterflies, which have a unique combination of features in that they are conspicuous (day-flying) and gentle (butterflies have no weapons, as Jim Scott observed[1]), which means that anyone can observe them and keep notes. Because so many people have observed butterflies for so many decades, we know how entire faunas (groups of animals living in the same place or region) have shifted and evolved over time. Butterflies have provided key insights into the ways that organisms respond to changing climatic conditions and human-modified landscapes.

However, if the question is "why do we do it?" then the value of butterflies and moths as objects of scientific study feels like far too easy an answer. This is because most of us who spend our time with butterflies and moths only discover their scientific utility at some later point in life, perhaps when we think about careers and long after we become addicted to the creatures. Instead, the answer might be as easy as this: We study butterflies and moths because we are charmed by them. Many of the authors in this book recall an early experience with a caterpillar in the grass or a large moth at the window that captivated them, apparently for life.

[1] Scott JA (2010) New terminology for describing mate-locating behavior of butterflies (and moths), with examples in Colorado. News of the Lepidopterists' Society 52:58–62.

But, you might object, surely butterflies and moths are essential parts of essential ecosystems and we have to understand them in order to keep the world functioning. Perhaps. If all caterpillars as well as adult butterflies and moths were to disappear from the planet tomorrow, there would indeed be consequences. Birds would suffer the loss of caterpillars to feed to their families, and millions of species of specialized flies and wasps that also depend on caterpillars as food for their young would go rapidly extinct. Plants, however, might be happier, because they would be spared the outrageous number of little bites they suffer every day. In any event, none of these things explain the addiction that attaches lepidopterists to their subjects.

Even though the answer might be as simple as I have suggested (we study moths and butterflies because we are charmed by them), many of us at public institutions use tax dollars, so we should be responsible for a more articulate answer. Here's my shot at an answer: Butterflies and moths are worthwhile subjects because the study of lovely and alien creatures satisfies our human need for riddles. Because Lepidoptera are both insanely diverse (possibly as many as a quarter million species) and also reasonably well understood (at least in terms of basic biology and ecology), they hit a certain sweet spot for the scientific imagination: plenty of riddles to go around, but the challenges feel just tractable enough to not be terrifying. By way of riddles, we can ask, among other questions: Why are most Lepidoptera so specialized in their feeding habits? Or why are some lineages of moths so much more diverse than others? Or how does the diversity of caterpillars affect the diversity of phytochemicals in plants and forests?

In addition to addressing those questions, I hope that I contribute to society by exposing others to these creatures that go about their lives without any concern or interest in human beings. When I have given presentations on insect diversity for elementary schools, occasionally I have been asked, often by a parent: "That's very interesting, but what do butterflies *do*?" Having fielded that question a couple of times, I have come to be pretty sure that what they are really asking is: "What do butterflies *do for me*?" The answer of course is that butterflies just *are*, and they do not care about you at all. For the kids at least, I think that perspective makes a few of them look around and consider the world in a slightly different way. Too many of them have somehow gotten the message that studying biology leads only to a career in medicine, but there are plenty of viable careers in science that start with a butterfly net.

Please do not assume that any of the other authors in this book would provide the same explanation for why they study butterflies and moths. Happily, the community of lepidopterists is just about (but not quite!) as weird and diverse as the butterflies and moths we study. If you are not a lepidopterist yourself, I think you will enjoy meeting the authors of these chapters. I hope that some of the joy they get out of butterflies and moths inspires you to take a second look at some strange creature in your backyard that does not care one whit for you (one of my favorites is shown in Fig. 1). If you are a lepidopterist, then we apologize for not inviting you to write a chapter! The community is large and we have left a great many people out; there was just no other way to go about it. Even to attempt a list of the people we wish we could have included would inevitably leave some people out. However, I suspect you (if you are a lepidopterist) will find someone you know in these chapters, and

Fig. 1 A small package full of surprises: the western pygmy blue butterfly *(Brephidium exile)*, is one of the smallest butterflies in North America. With a wingspan of typically less than 2 cm, adults can be mistaken for swarms of flies as they fly low to the ground. The caterpillars are tended by ants that protect them in exchange for sugary rewards, and consume a number of plants that include the exotic (nonnative) tumbleweeds, *Salsola* species, famous from cowboy movies. Despite their small size, the adults are quite far ranging, which in combination with rapid generation times, allows the species to seasonally spread across enormous distances, even into areas that are too cold for it to maintain permanent populations. (Illustration by MLF)

hopefully that someone has written down a story that will preserve a bit of the legacy of late twentieth-century and early twenty-first century lepidopterology.

M. L. Forister
University of Nevada, Reno

Matthew L. Forister is an evolutionary ecologist in the Biology Department at the University of Nevada, Reno. He received a BA in English writing from the University of San Francisco, spent 2 years with the Peace Corps in Ukraine, and then earned a PhD in ecology from UC Davis. He studies herbivory, diversity, and hybridization, and has worked with different plants, animals, and fungi across temperate and tropical ecosytems, but particularly loves the blues, coppers, and hairstreaks (family Lycaenidae) and their humble but fascinating caterpillars and the ants that keep them safe. When not chasing butterflies, he favors old novels, the mountains of the Great Basin, and hanging out on the porch with his family, Beth and Catalina.

Introduction

I never liked insects, so I never paid attention to moths and only occasionally noticed butterflies. Caterpillars rarely entered my realm of consciousness. My first trip to the tropics in 1991 changed all of that. I was in Costa Rica with a group of graduate students on my second evening ever spent south of the Tropic of Cancer. We were late on our way back to the research center, where we were expected for dinner, and the many biological distractions that make up a tropical forest were slowing us down considerably. By far, the most amazing of these distractions was the giant tropical ant, *Paraponera clavata*, with a large green and black caterpillar in its mandibles. Not only had I never seen an ant so large—as great as 3 cm from head to stinger—but also had I rarely witnessed predation in action. Both predator and prey were more elaborate and beautiful than any of the myriad National Geographic photographs that I had seen over the years—photographs of classic pairings: lynx–snowshoe hare, jaguar–peccary, fer-de-lance–agouti, or shark–human. The caterpillar was still struggling, and as darkness set in and the other students were realizing they should not have followed me to this dark corner of the woods, I plucked the caterpillar out of the mandibles of the beautiful giant ant and tucked it into my front shirt pocket. We were lost in an unknown forest at night and it was somehow my fault, but as we thrashed around trying to find some sort of trail or road, all I could think was, "I can't wait to photograph this caterpillar and figure out what it is and what it eats." Thus began a long love affair with immature Lepidoptera, the plants they eat, and the animals that eat them.

What attracts us to moths (for me, this term includes the "butterfly" superfamily, Papilionoidea) and how has this attraction enriched society by contributing to science, art, literature, and popular culture? This question has a thousand answers and there are literally thousands of personalities that can provide substantive and entertaining responses based on lifetimes of experience. For *Lives of Lepidopterists,* we attempted to compile some of the well-developed narratives that are out there, hoping that they will provide a glimpse into the experiences and outcomes of a life studying the scale-winged insects and their eggs, caterpillars, and habits. I think we succeeded in capturing a great mix of adventure, humor, epiphanies, history, and the extraordinary joy that are all a part of studying nature. However, it was also impossible to make a short list of authors who could contribute to such an endeavor, and our haphazard approach falls short of including the potential volume and richness of prose that can be assembled. In particular, a more balanced view of lepidopterists would include greater cultural, geographic, and occupational diversity, and despite our efforts, many potentially great contributors to a more diverse view of life were unable to participate. One exemplary omission is the great naturalist Daniel Janzen.

I first met Janzen just a couple of weeks after I had managed to get an entire cohort of tropical ecology students lost in the forest at night because of my attraction to a little black and green geometrid (inchworm) caterpillar. Dan was larger than life, and after reading a couple dozen of his more entertaining and thought-provoking papers, I was not disappointed when he told me that my planned graduate research was completely without merit and was based on a sore misconception that there was such a thing as a "generalist" herbivorous insect. This pronouncement was made within 15 minutes of meeting me, and based on his confidence and thorough justifications, I knew right away that I would like to embark on caterpillar collaborations with this man. Decades later, and after learning a great deal from Dan and even publishing some papers with him, I invited him to write a chapter for this book, then entitled, *The Secret Lives of Lepidopterists.* Dan's first response was that there was absolutely nothing secret about what he and Winnie (his wife and collaborator, Winnie Hallwachs) did as lepidopterists, and if there was, he certainly would not put it in our book. Then he stated that he would absolutely refuse to participate if the book was a printed product instead of an online tome (his preferred media). Despite the poetic intent of the word, "secret," we agreed to delete it, but both Matt and I have bachelor's degrees in English and we love traditional books, so we refused to change the format and Janzen berated us for creating more termite food. Although we are sorry that Dan and many other great lepidopterists could not contribute their experiences and insights to this book, we do hope that this work provides entertainment and information to a diverse audience for decades and centuries to come. To some, it may seem that studying Lepidoptera could not possibly yield enough entertaining stories or adventures to fill a traditional book, but in my experience it is filled with exciting discoveries, great adventures, and wacky personalities.

Since my own tropical introduction to Lepidoptera 25 years ago, I have had notable adventures associated with my research-based travels, including being held at gunpoint multiple times, car wrecks on tropical mountain roads, spending nights lost in the forest, and stepping on more than a few pit vipers. I have also had plenty of exciting epiphanies in the field, lab, office, and museum that have kept me intellectually challenged. Most important, I have had the great fortune to meet an amazing array of personalities who fall under the general title of "lepidopterist," and whose lives could provide copious material for popular books or movies. To give a sense for why we think that those who have spent a large portion of their lives studying moths have great stories to tell, I will slip in just a few examples of adventurous and interesting lepidopterists I have met from my travels for research or teaching, starting with another short tropical story—about the coleopterist, Frank Hovore, an all-around great entomologist and a fearless collector. In the early 90s, Frank's life was saved by Louis LaPierre, another avid collector. At a remote site in Costa Rica, Frank had lunged for a swallowtail butterfly with his large insect net but instead hit a power line and was electrocuted - Louis used CPR to bring Frank back to life. Frank studied beetles, but even coleopterists love butterflies, and he was no stranger to capturing butterflies with that net. Years later, in 2006, I was surprised to bump into Frank with a similar net, walking up a dirt road in the Andean cloud forest in Ecuador. He was in a fabulous mood as he showed me a beautiful day-flying notodontid moth that he had just captured (along with a dozen or so beetles), and then he disappeared up the road in search of more insects, inspiration, and adventure. I found out later that Frank died of a heart attack that same day—perhaps it is a fanciful notion, but some said that his heart finally gave out after that terrible collecting-induced shock years earlier.

Another adventurous lepidopterist who I met on that dirt road in Ecuador was Suzanne Rab Green, who works with collections of moths at the American Museum of Natural History (AMNH). When she is not sailing around the world for her "other job," or sneaking off to a secret high spot that offers the most unique view of New York City, Suzanne can show visiting lepidopterists some very special projects at AMNH, including a large collection of reared tiger moths from the tropics, or a collection of some of Nabokov's butterflies from one of his long road trips. Suzanne also introduced me to Padre Piñas and Giovanni Onore in Ecuador. The Jesuit priest, Padre Francisco Piñas Rubio, is an avid amateur collector who put together an impressive collection of tropical moths and an equally impressive set of tales about how the collection came to be. Padre Piñas made artful wall hangings from some of the butterflies he collected and had organized all his collections in aesthetically appealing arrangements, but they were difficult for me to use. I actually spent more time seeking out his colleague, Giovanni Onore, who when I met had just been shot in the leg by a bandit as he was leaving a bank in Quito with funds for his next trip to the cloud forest—the bullet had grazed his head, so he was happy to be alive. Onore is most interested in beetles, but since arriving in Ecuador in 1980, he has been an incredible contributor to the study of Lepidoptera—and more generally to entomology—in Ecuador and has created an entomological collection with close to two million specimens at the Pontificia Universidad Católica del Ecuador, including an important collection of Lepidoptera. He now lives at the top of a hill with a good view but spends much of his time at a reserve where he is the director of Fundación Otonga, which is a beautiful cloud forest with great hilltop views of the surrounding Andes.

"Hilltopping" is something that both butterflies and lepidopterists like to do, whether it is for reproduction, finding butterflies, or simply the nice views. For example, Vitor Becker also lives in a beautiful hilltop home in the Atlantic Forest in Brazil. I spent hours walking up the terribly steep dirt and stone roads to visit his house, and I marveled at both the colorful forest around his home and his carefully curated collection of 300,000 tropical moths. Vitor sent me a few entertaining stories to include in this book, but they were a bit off color, so he agreed to have his colleague, Ivone Diniz, write about him in her contribution to the book. Anyone who knows Vitor might appreciate the fact that some of his stories should remain an oral tradition. Vitor was introduced to me by Jim Miller, who left his job as curator of Lepidoptera at the AMNH to become a rock star—he helped form the band, Donna the Buffalo. To this day, Jim remains both a well-known musician and an important lepidopterist—in fact, as part of a 1000+ page monograph on special moths called dioptines, he named the species of day-flying moth that Frank Hovore showed me on that mountain road in Ecuador.

Some of the best stories about lepidopterists across the Americas come from Arizona. There I met a crew of self-educated collectors who were some of the most fanatical scientists I have ever encountered. Someday I hope that there will be a book about this crazy bunch of moth lovers. Among this crew are many strong, quiet adventurers, who prefer to remain unnamed, who spend much of their free time scouring every inch of the Arizona borders, looking for rare moths and undiscovered caterpillars. One has been arrested several times coming across the border from Mexico, another has caused fist fights by continually "stealing" specimens from light traps set up by others, and several others always carry guns for protection because they venture to dangerous parts of the border. It turns out that at least one of these moth collectors has a satellite security system that can bring law enforcement officers to her exact location in a matter of minutes. One night in Florida Canyon, Arizona, after the moth lights had long been abandoned, I woke to the loud noises made by a passel of officers with M-16s and additional weapons, confronting one of my moth-collecting friends, who was towering over them, standing his ground in his underwear at the door of our remote caterpillar-rearing shed. Someone's warning device had malfunctioned and the officers had received the alarm. Fortunately, no caterpillars or lepidopterists were harmed in the incident.

In field sites throughout the Americas, I have had entertaining and enjoyable encounters with many great lepidopterists; in fact, there are too many to list here (plus I fear that I would accidentally exclude somebody important). All of these scholars of caterpillars, moths, or butterflies have amazing stories to tell, but not all of them could be included. Hopefully, their stories will continue to be told.

There are two final stories that I cannot leave out here. They are not about lepidopterists, rather they are about some of the most important contributors to the study of Lepidoptera—local field assistants and citizen scientists. I had hoped that Janzen would be able to tell the story of the individuals that he and Winnie call "gusaneros"—local Costa Ricans who were hired, without any prior training, to collect caterpillars on their 45-year project rearing caterpillars in the Guanacaste Conservation Area. These gusaneros created the greatest ecological database on Lepidoptera ever assembled and have their own stories to tell. I followed this model when I started a much smaller version of Dan and Winnie's caterpillar-rearing project that included the help of both field assistants and citizen scientists, and individuals from both these groups have worked with this project at sites across the Americas and include some of my closest friends. Gerardo Vega Chavarria was one of the assistants in Costa Rica, and although he was more of a botanist than a lepidopterist, he was the quintessential "gusanero." One day Gerardo brought me to his favorite spot off-trail in the forest—only about an hour away from the trail, but still a spot that is rarely trampled by humans. As we were sitting there, enjoying the view, Gerardo suddenly jumped up, yelling as he ran forward. Fortunately, I immediately followed. Somehow, he had heard the cracking of a branch up in the canopy, and the limb that crashed down precisely on the spot where we had been sitting would have

Fig. 1 *Acharia hyperoche* (Limacodidae) - the spines are urticating! The biology of this great family of caterpillars is enough to attract anybody to the study of Lepidoptera.

easily crushed us both. My heart was racing as we returned to the spot to examine the offending tree branch, and to my amazement, the leaves were covered with about 100 beautiful spiny green and red caterpillars—stinging saturniids (similar to the limacodid depicted in Figure 1). Gerardo smiled and said, "that is how I collect Lepidoptera." Years later, when Gerardo died, Deborah Letourneau and I paid to have the nearest trail marker named after him.

Finally, Ginny Knox worked briefly on our caterpillar-rearing project in Costa Rica. She was a paying volunteer—one of over 1000 Earthwatch volunteers who have collected caterpillars at seven sites that I maintain with colleagues and students from Northern California, down to Southern Ecuador. Ginny was 83 and had just gone through hip replacement surgery, so she worked almost exclusively in our ambient caterpillar-rearing lab. Much to my dismay, I discovered that she was sneaking into the lab every morning to set free any adult moths or butterflies that had emerged from the pupa because she could not bear the thought that we would kill them for identification and voucher purposes. She was such a sweet person, and I could not let her leave that site without seeing some special part of the forest; so on the last day, I helped her into the large platform of the cargo bicycle and rode several kilometers into the forest with her to a hand-operated cable car crossing a river. I managed to get her into the car and we went to the middle of the Sarapiqui River and sat hanging, watching butterflies for an hour. We mostly watched the great iridescent blue butterfly, *Morpho peleides*, flitting around in the sun. When it finally landed on our small car, I looked over at Ginny and tears were streaming down her face. No words were necessary. And it was at that point that lepidopterology, and the obsessions of lepidopterists, finally made sense to me.

Lee A. Dyer
University of Nevada, Reno

Lee A. Dyer is an ecologist who has worked with Lepidoptera—focusing on immature stages—in tropical and temperate ecosystems for the past few decades. He received a BSc in biochemistry and a BA in english from the University of California (UC) Santa Barbara and then spent 6 years traveling, rock climbing, writing poetry, and working on environmental issues before deciding to go to graduate school. His PhD research at the University of Colorado, Boulder, examined chemically mediated interactions between plants, herbivores, and their natural enemies and included work in Costa Rica, Colorado, and California. Lee spends his free time looking for caterpillars, hanging out with his family, rock climbing, listening to music, drinking red wine, writing poetry, and reading books.

Acknowledgments

Parnassius smintheus. Illustration by Anne Espeset.

Special thanks to everyone who has contributed a chapter to this book, as well as to those who attempted to get us a chapter. We also thank the graduate students of the Ecology, Evolution, and Conservation Biology graduate group at the University of Nevada, Reno, for contributing illustrations. For feedback on our plan to collect the stories of lepidopterists, we thank the extended lab group in the last couple of years: Angela Smilanich, Lora Richards, Jane Dell, Anne Espeset, Andrea Glassmire, Josh Harrison, Josh Jahner, Tara Langus, Will Lumpkin, Colin Morrison, Nick Pardikes, Gift Poopat, Su'ad Yoon, and others (thanks in particular to Josh Jahner for saying "Yeah, I'd buy that" when we initially floated the idea). Gabrielle Blaustein took on the index and really helped us out. Research and outreach, including the production of this book, in the Dyer and Forister labs have been supported by grants from the National Science Foundation (DEB-1020509, DEB-1050726, DEB-1145609, DEB-1442103). Finally, thanks to the gusaneros, volunteers, students, teachers, museum curators, journal editors, reviewers, collaborators, field stations, guidebook authors, and all of the Lepidoptera, their host plants, and their enemies.

Contents

Contributors

Annette Aiello Smithsonian Tropical Research Institute, Ancon, Balboa, Republic of Panama

Greg Ballmer University of California, Riverside, CA, USA

Pedro Barbosa University of Maryland, College Park, USA

M. Deane Bowers University of Colorado, Boulder, USA

John Brown Smithsonian Institution, Washington, DC, USA

Roger L. H. Dennis Staffordshire University, UK

Phil DeVries University of New Orleans, New Orleans, LA, USA

Ivone Rezende Diniz Universidade de Brasília, Brasília, DF, Brazil

Paul R. Ehrlich Stanford University, USA

Lawrence E. Gilbert Department of Integrative Biology, University of Texas, Austin, USA

Harold F. Greeney Yanayacu Biological Station, Napo, Ecuador

Ilkka Hanski University of Helsinki, Finland

Sangmi Lee Arizona State University, Tempe, USA

Carla M. Penz University of New Orleans, New Orleans, Louisiana

Jerry A. Powell University of California, Berkeley, USA

Robert Michael Pyle Washington, USA

Mark Scriber Michigan State University, East Lansing, MI, USA

Art Shapiro University of California, Davis, USA

Michael C. Singer Plymouth University, Devon, UK

Felix Sperling University of Alberta, Edmonton, AB, Canada

Part I
How Did We Get Here?

Principium erit mirari omnia, etiam tristissima.
Carolus Linnaeus, *Philosophia Botanica*

For Linnaeus, any study in biology or natural history, including the study of the countless species of moths and butterflies he named, starts with marveling at all things, even organisms that seem common and drab, like armyworms. There are as many routes to becoming a lepidopterist as there are scientists who study moths. Most of the chapters in this book give some insight into how lepidopterists arrive at their passion for these insects, but the first three provide a nice mix of stories of starting points for discovery.

LAD

An adult armyworm, common (and not usually admired) throughout much of North America. Illustration by MLF.

Chapter 1
From Caterpillars to Chemistry

M. Deane Bowers

Introduction

I remember v-e-r-y slowly putting my hand through the fence into my neighbor's yard to capture my first black female tiger swallowtail; no net available. I was nine. It was awesome! I still have the specimen with its sewing pin through the thorax (thankfully not the abdomen, as I was pretty inept in those days, Fig. 1.1) and a label the size of a business card. Those were the early days of excitement and fascination as I learned about butterflies and other insects.

Growing up in Florida (before it became as developed as it is now) was wonderful for a budding lepidopterist; there were so many different habitats and an incredible diversity of insects. My bibles were *A Field Guide to the Butterflies* by Alexander Klots (1958) and *The Amateur Naturalist's Handbook* (Brown 1948), both of which I still have. I constantly had checked out from the library *The Butterfly Book* (Holland 1898) and *The Moth Book* (Holland 1903), both of which I now own. From these inspiring resources, I learned how to collect, identify, and prepare butterflies and moths, how to keep a field notebook, and how to observe nature and think about doing experiments. I raised caterpillars in my bedroom and put together a weather station in my backyard. My parents got me my first butterfly net and encouraged me. I made butterfly jewelry by painting clear nail polish over butterflies I had collected and spread and by attaching safety pins to them.

High school intruded, but my fascination survived. My junior year, there was the big decision: try to capture the HUGE sphinx moth at the gas station light (which I learned was *Pseudosphinx tetrio*) or leave it and go with my friends. I made the right choice and captured it. I had been, and still was, hooked.

M. D. Bowers (✉)
University of Colorado Museum, University of Colorado, UCB 334, Boulder, CO 80309, USA
e-mail: deane.bowers@colorado.edu

Department of Ecology and Evolutionary Biology, University of Colorado, UCB 334, Boulder, CO 80309, USA

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_1

Fig. 1.1 Female tiger swallowtail (*Papilio glaucus*, Papilionidae). Note the sewing pin instead of the more appropriate insect pin. (Photo by Brian Lobbes)

From Caterpillars to Chemistry

The move from rearing and collecting to thinking about butterflies and moths in a more scientific way began in college, when I did a small project looking at how feeding on different plants affected the growth and development of painted lady caterpillars and was encouraged to pursue my interest in insects. I was able to take some entomology courses at the nearby University of Massachusetts, where, despite being told that "women can't be entomologists, except possibly taxonomists," I decided that I could. My fascination with butterflies and moths led me to apply to graduate school in entomology, but I found that most entomology departments wanted students to work on projects that were ongoing in the labs of faculty members. So, I declined offers to work on alfalfa weevils or blowflies and ended up in the Department of Zoology at the University of Massachusetts. I had not had much experience with research as an undergraduate and was not sure exactly how to go about deciding what to focus on for my graduate research. My advisor, Ted Sargent, a specialist on *Catocala* (Noctuidae), told me to spend my first summer reading and looking for potentially interesting systems, finding something that excited me.

And I did! That first summer, I discovered the Baltimore checkerspot, *Euphydryas phaeton* (Nymphalidae) (Fig. 1.2), feeding in swampy habitats where its host plant, Turtlehead, *Chelone glabra* (Plantaginaceae), grew. I was fascinated by the brightly colored orange and black caterpillars and the striking black, red, and yellow adults, characteristics suggesting that this species might be advertising the fact that it was unpalatable. Indeed, Samuel Scudder, in 1889, first suggested that this species was unpalatable, noting that:

> …the butterflies are not touched by birds, probably having some quality obnoxious to smell or taste, and the caterpillars seem to have a similar immunity. …it would seem as if so sluggish a butterfly would soon be exterminated by birds, did it not possess some obnoxious character, for it is I think, the most sluggish butterfly we have.

My first attempt to turn my interest in this butterfly into a dissertation was deemed to be too much natural history by my committee—and they were right. I persevered, however, and ultimately, my thesis research on *E. phaeton* and other members of the genus investigated host–plant relationships in *E. phaeton* and showed that this species, as well as other species in the genus, were unpalatable to blue

Fig. 1.2 Life history of the Baltimore checkerspot (*Euphydryas phaeton*, Nymphalidae). Clockwise from *upper left*: Adult, egg mass on turtlehead (*Chelone glabra*, Plantaginaceae), pre-diapause larvae on web, post-diapause larvae on *C. glabra*. (Photos by Deane Bowers)

jays (Bowers 1980, 1981). It was the natural history of these relationships that first piqued my interest and that then informed the research.

This research introduced me to the field of chemical ecology. I was fascinated and inspired by the work of people like Miriam Rothschild, Thomas Eisner, Gottfried Fraenkel, Jane Van Zandt Brower, Lincoln Brower, and Vincent Dethier (these last two serving on my doctoral advisory committee), as well as many others. This field was just beginning in the 1960s and 1970s as ecologists and evolutionary biologists started talking to natural products chemists. The publication of books like Harborne's (1972) *Phytochemical Ecology,* Sondheimer and Simeone's (1970) *Chemical Ecology,* and van Emden's (1973) *Insect Plant Relationships* was also happening and changing how chemical compounds in plants were viewed: They were starting to be thought of as more than just the waste disposal system of plants (Fraenkel 1959, 1969).

Although I was unable to do any chemical analyses in the course of my dissertation research, my thesis concluded with the idea that the host–plant relationships and unpalatability of *Euphydryas* were due to a particular group of chemical compounds that were found in most of the host plants of this genus, the iridoid glycosides (Bowers 1979). These compounds were found in all of the host plants of North American *Euphydryas* and were noted to be very bitter (Hegnauer 1973; Kubota and Kubo 1969). These observations suggested to me that it might be iridoid glycosides that were responsible for not only host plant specificity but also the unpalatability of these butterflies. Subsequently, these ideas with which I concluded my thesis were supported by the experiments that were begging to be done. I found that larvae of *E. chalcedona* used iridoid glycosides as larval feeding stimulants (Bowers 1983) and that, indeed, the unpalatability of checkerspots was due to sequestration of these compounds by larvae and their retention to the adult stage (Bowers and Puttick 1986; Bowers et al. 1992). The chemical ecology of checkerspots and other butterflies and moths that specialize on plants containing iridoid glycosides has continued to be a major focus of much of my research and the source of much of my passion for biology.

My 2-year postdoc with Paul Ehrlich introduced me to California (I had never been west of Ohio) and the western checkerspots. I was able to explore northern California, Oregon, and Washington in the search for checkerspot populations. On one of those trips, I ran into the results of the Mount St. Helens eruption! I was out in the middle of nowhere, with no radio reception, so had not realized what had happened. I started seeing piles of white dust on the side of the road, and when I reached a town, I found out what had occurred. In addition to some great fieldwork opportunities, it was there that I was able to do some of the experiments showing that iridoid glycosides were feeding stimulants for checkerspots and to begin working on another nymphalid that is an iridoid glycoside specialist, the buckeye *Junonia coenia*. This species has also served as a great study organism for many experiments.

I was fortunate in having a lot of freedom as a postdoc and to be able to learn from another postdoc, David Lincoln, about some of the basics of plant secondary chemistry. I also had the opportunity to attend the first Gordon Conference on the "Chemical Aspects of Plant–Animal Interactions," where I met many of the people whose work I had read, including Miriam Rothschild, who had been such an inspiration to me. This conference really clinched my research focus in the field of chemical ecology.

From California I moved back to the east coast for a beginning assistant professor position at Harvard, where I was the curator of the Lepidoptera collection and, with another curator, ran the entomology section. This was certainly an interesting time. Not only was I a woman entomologist, in a time when the field was dominated by men, but for 2 years I was the only woman in the department at Harvard. I will admit that I got tired of being introduced as "our pretty little lepidopterist." However, the collection there was amazing and I grew to love the museum part of my job. Despite some of the difficulties, my time there solidified my interest in the chemical ecology and evolution of insect–plant interactions and also my enjoyment of the museum side of entomology.

I got to a point in my research, however, when I realized that I either had to go learn some more chemistry and chemical techniques or I had to start asking different kinds of research questions. Through a National Science Foundation (NSF) program, "Visiting Professorships for Women in Science," I had the great good fortune to spend a year working in the lab of Frank Stermitz, a natural products chemist at Colorado State University, who also loved biology. That year changed my life! One of the focal groups of compounds in his lab was none other than iridoid glycosides!! At that time, there were no women in the Chemistry Department there, and they thought I was kind of strange: I had cages of butterflies hanging in the window of my office to try to get them to mate and plastic containers of caterpillars everywhere. But Frank Stermitz and his graduate students helped me learn a diversity of techniques that I was able to integrate into my own research program… and it took some patience on their parts. I learned so much. While I was there, I got to isolate pure iridoid glycosides and learned about nuclear magnetic resonance analysis, gas chromatography, and high performance liquid chromatography. I really, really wanted to discover a new iridoid glycoside, but I never did. Instead, I analyzed lots of known ones and used the knowledge that I gained there to integrate chemical analysis into my research program.

From the east coast, I was able to return to Colorado in 1989, when I began a position as a faculty member at the University of Colorado. Here, I was jointly appointed between the Museum of Natural History, where I was the curator of entomology, and the Department of Ecology and Evolutionary Biology. This was the perfect place for me: although not a systematist (as most curators are), I had developed a love for the museum side of entomology and was thrilled to be able to be in charge of a collection. It was also here that I gained a better understanding of the plant side of plant–insect interactions, and I began to view plants as something more than just caterpillar food.

My research has retained its focus on the chemical ecology and evolution of plant–insect–enemy interactions, with a clear predilection for members of the Lepidoptera. My major focus has been on temperate species, especially taxa that are involved with plants containing iridoid glycosides and the effects of those compounds at multiple trophic levels, the herbivores, as well as predators, parasitoids, pathogens, pollinators, and mutualistic fungi. This research has shown how plant secondary metabolites influence not only the interactions of plants with other organisms but higher trophic level interactions as well.

Advice for Future Lepidopterists

The Lepidoptera provide a diversity of lifestyles, interactions, and relationships with which to explore the dynamics of the natural world. Of all groups of insects, they are probably the best known; however, there is still a wealth of information to be discovered. The Lepidoptera have been used as model organisms for some of our most important discoveries in ecology and evolution, providing insights into such topics as mimicry, natural selection, speciation, plant–animal interactions, and conservation. They can be considered charismatic "microfauna" and, as such, provide a wonderful means of captivating both students and the public.

Some of the most important information I have used in my research has come not from professional lepidopterists but from amateurs. Indeed, most lepidopterists are not professionals; the number of amateur lepidopterists far outweighs the number of professionals. While one may quibble about the precise definition of an amateur, an amateur is essentially someone who is not paid to do the same job as a professional (who is paid). Yet, often these nonprofessional lepidopterists know more about the natural history, behavior, and ecology of butterflies and moths than any professional. And they have this knowledge because they love the natural world. They collect, photograph, and observe. The contributions of amateur lepidopterists are evident in their publications, books, and collections. As an amateur, there is much that you can add to our understanding of the biology of butterflies and moths; for example, describing and photographing life histories, documenting behavior, rearing parasitoids, participating in 4th of July butterfly counts, putting together a well-documented and well-curated collection. Several articles have highlighted the value and potential contributions of amateur lepidopterists (e.g., Munroe 1960; Ferris 1986; Miller 1986): there is much you can do!

For those interested in a future in lepidopterology, whether professional or amateur, get out into nature, meet other lepidopterists, participate in butterfly counts, get involved in restoration projects, and attend regional meetings or the national meeting of the Lepidopterists' Society. Joining one of the societies that focuses on Lepidoptera is also a great way to meet people and find out what kinds of projects are going on; for example, there is the Lepidopterists' Society, the North American Butterfly Association, and the Xerces Society. There are also many smaller, local societies. You can also take a look at the Butterflies and Moths of North America website (http://www.butterfliesandmoths.org), which has lots of resources about butterflies and moths, including identification, and lists some of the local lepidopterists societies.

If you are interested in a career as a professional lepidopterist, there are many possibilities. Again, making contact with other lepidopterists is very important. Professional lepidopterists can work at museums, at colleges and universities, for agencies such as the United States Department of Agriculture (USDA), and the Nature Conservancy. Their disciplinary specialties range from the systematics of particular groups to behavior, ecology, physiology, development, evolution, and interactions with other groups of organisms such as plants, predators, pathogens, and parasitoids. Not all who work with Lepidoptera would call themselves lepidopterists; their focus may be more on developmental regulation or restoration of native habitats. Yet, they work with butterflies or moths. If you want a future as a lepidopterist, think about what you want to do, meet other lepidopterists, and get the training that will best prepare you for your future goals. Go for it!

For myself, I consider myself particularly fortunate; being a lepidopterist is not only my job, but also something that brings me great satisfaction and joy!

Acknowledgments With thanks to the many people who have influenced my development as a lepidopterist and chemical ecologist. My doctoral advisor, Ted Sargent, encouraged me to find a project that inspired me and let me work on butterflies, providing much support and encouragement along the way. My postdoctoral advisor Paul Ehrlich introduced me to the butterflies of the West and gave me the freedom to work on my own projects. Frank Stermitz and his students introduced me to the chemical side of chemical ecology and my time in his lab really changed the course of my research. Last, but definitely not least, thank you to my students, both past and present, you have and will always continue to inspire me.

References

Bowers MD (1979) Unpalatability as a defense strategy of checkerspot butterflies with special reference to *Euphydryas phaeton* (Nymphalidae). Ph.D. Dissertation, University of Massachusetts

Bowers MD (1980) Unpalatability as a defense strategy of *Euphydryas phaeton* (Lepidoptera: Nymphalidae). Evolution 34:586–600

Bowers MD (1981) Unpalatability as a defense strategy of western checkerspot butterflies (*Euphydryas* Scudder, Nymphalidae). Evolution 35:367–375

Bowers MD (1983) Iridoid glycosides and larval hostplant specificity in checkerspot butterflies (*Euphydryas*, Nymphalidae). J Chem Ecol 9:475–493

Bowers MD, Puttick GM (1986) The fate of ingested iridoid glycosides in lepidopteran herbivores. J Chem Ecol 12:169–178

Bowers MD, Stamp NE, Collinge SK (1992) Early stage of host range expansion in a specialist insect, *Euphydryas phaeton* (Nymphalidae). Ecology 73:526–536

Brown V (1948) The amateur naturalist's handbook. Little, Brown and Company, Boston

Ferris CD (1986) Presidential address, 1986: unexplored horizons—the role of the amateur lepidopterist. J Lepid Soc 40:247–254

Fraenkel G (1959) The raison d'etre of secondary plant substances. Science 139:1466–1470

Fraenkel G (1969) Evaluation of our thoughts on secondary plant substances. Entomol Expl Appl 12:473–486

Harborne JD (Ed) (1972) Phytochemical ecology. Academic Press, New York

Hegnauer R (1973) Chemotaxonomie der pflanzen, vol 6. Berkhauser, Basel

Holland WJ (1898) The butterfly book. Doubleday, Page & Company, New York

Holland WJ (1903) The moth book. Doubleday, Page & Company, New York

Klots AB (1958) A field guide to the butterflies of North America, East of the Great Plains. Houghton Mifflin Company, Boston

Kubota T, Kubo I (1969) Bitterness and chemical structure. Nature 223:97–99

Miller LD (1986) Presidential address, 1984: a tribute to the amateur. J Lepid Soc 40:1–7

Munroe E (1960) President's annual address, 1959: professional and amateur research in Lepidoptera. J Lepid Soc 14:1–4

Scudder S (1889) The butterflies of the Eastern United States and Canada. W.H. Wheeler, Cambridge

Sondheimer E, Simeone JB (1970) Chemical ecology. Academic Press, New York

Van Emden HF (Ed) (1973) Insect/plant relationships. Wiley, New York

M. Deane Bowers is a professor in the Department of Ecology and Evolutionary Biology as well as the museum's curator of entomology at the University of Colorado, Boulder, USA. Deane received her bachelor's degree in zoology from Smith College and her PhD at the University of Massachusetts in 1979. After a 2-year postdoc at Stanford University, she started her first job in the Museum of Comparative Zoology at Harvard University, where she was the curator of Lepidoptera. She came to the University of Colorado in 1989. Her research interests are in the ecology and evolution of insects, insect chemical ecology, plant–insect interactions, interactions of caterpillars and natural enemies, and the biology of the Lepidoptera. She grew up in Florida, where she started her fascination with Lepidoptera and nature at an early age. Deane has many diverse hobbies outside of her professional work and enjoys gardening, hiking, dancing, cooking, and the arts. She is a great mentor for undergraduate and graduate students around the world.

Chapter 2
A Reflection on the Career: Following a Path to Moths and Butterflies

Pedro Barbosa

Because I was born in a small rural town along the southeastern coast of Puerto Rico, I was surrounded by nature and caterpillars. But having been taken to New York City at the age of three, I was not really aware of these magnificent creatures during those early years. For the few of us who grow up in urban environments like Spanish Harlem (Fig. 2.1, Upper panel) but love butterflies, seeking butterflies and moths is not exactly like looking for moths and butterflies in the Amazon, or the forests of New Guinea, but it is challenging and scary in its own way. I would visit those exotic places many years later, but as a youngster I could not even imagine those places. But how does anyone become seduced by butterflies and moths in the middle of a concrete jungle? As a youngster in the city, the insects that I was most exposed to, up close and personal, were flies, ants, cockroaches, and bedbugs.

As a kid in the city, flies and ants were interesting little critters, and I could look at them through a toy microscope that my uncle got me; cockroaches were inevitable coinhabitants that seemingly could not be avoided. Unfortunately, they were also a constant icon of failure for some reason I cannot remember, and the bedbugs just made me itchy and sleepless (Fig. 2.1, Lower left panel).

Still I was fascinated by insects. The fascination was not an adaptive survival trait, but a source of ridicule and bullying by other youngsters who enjoyed inflicting pain. Luckily, one very effective way to avoid those other youngsters was to spend a lot of time at the zoo, libraries, and museums. Hoodlums, whether they were random individuals or gangs, such as the Young Lords (Fig. 2.1, Lower right panel) in the 1950s and 1960s, did not spend much time in any of these places.

What does this have to do with butterflies and moths? Well, it was on one of these trips to a museum that I saw a display of the Lepidoptera collected in New York City. It was my first introduction to moths and butterflies and to my beloved luna moth. It was a very dusty, old display. I never actually did see any of these species in the display, flying around, but it made an impression on me and started a lifelong love. I needed to seek out places where I might see these wonderful

P. Barbosa (✉)
Department of Entomology, University of Maryland, College Park, USA
e-mail: pbarbosa@umd.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_2

Fig. 2.1 *Upper panel*: Homes and stores in Spanish Harlem (http://www.skyscrapercity.com/showthread.php?t=504084). *Lower left*: reaction to bedbug bites. *Lower right*: The Young Lords—the dominant youth gang in Spanish Harlem; a group consisting of children of migrant Puerto Ricans who came to the country in the 1930s and 1940s. (http://www.latintrends.com/?s=the+young+lords&submit=Search)

creatures and other insects as well. So, I had no other choice. I walked across the George Washington Bridge just to find some green grass, trees, maybe a couple of flowers, and of course insects, many of which were moths and butterflies. Growing up in New York City I did not see much nature near my house, and since my family did not own a car, I would frequently walk across the George Washington Bridge to New Jersey to find more nature and less concrete (Fig. 2.2). Apart from wanting to escape the concrete jungles of New York, I loved being around what was the closest to the "natural world" and observing what was there and what they did. Not in my wildest dreams did I ever imagine that my interests in biology and insects, in particular, could become anything resembling a job. I had no idea, as a youngster, that anyone would pay you for doing what you love.

Fig. 2.2 The George Washington Bridge: the long trek from Spanish Harlem to New Jersey

My first realization that an interest in entomology could become a job and a career did not occur until I was an undergraduate in college. Furthermore, that realization came about in the most unusual way. I attended the City College of New York, a school on the edge of Harlem. I planned on becoming a medical doctor, but soon realized I disliked the reality of being a pre-med at that time. Despite this, I always had a passion for science. Although I was a "poor student," this was not the case when I took biology courses. In other words, I only did well in the classes I liked, but those classes were all biology related. I loved those courses and so was interested. As a result doing well in the courses came easy to me because I was learning about things I cared about.

As I moved through college, I drifted away from the goal of becoming a doctor, even though I had no idea how anyone could have a career or make a living by loving and working with insects. But luckily, life is what happens while you are making other plans. In college, as an undergraduate, two life-changing experiences brought me back to my love of insects. As an undergraduate, I took just about every biology course offered. In those courses, I interacted with pre-meds. Let us say that the people who were attracted to that career path were clearly neither my kind of people nor the type of people I wanted to be with. Second and most important, as well as oddly enough, I was lucky that many of the biology teachers I got to know had a background in entomology or botany, which further drew me to both those interests. I got an opportunity to talk to these professors, not so much about the particular courses they taught but about their love of insects and plants. Who knew that decades later I would be totally absorbed in plant–insect interactions, in particular, and the magnificence of caterpillars and Lepidoptera–plant interactions, in general.

At any rate, the goal of being a doctor disappeared and the beginning of a lifelong love of insects began. Unfortunately, with an attitude of working hard only in courses I loved, and not so much on those I did not really like or "get," was not the best strategy for moving into a career of any kind. As one would predict, I did not have the best grade point average (GPA) or even an OK GPA. I mention this because as one might predict I did not really have many options regarding the graduate program to which I might be accepted. Thus, at the end of the application process I only had three choices: Texas Tech University, University of Hawaii, and University of Massachusetts (UMASS) at Amherst. My thinking at the time was that, given that in those days, as far as I was concerned, Maryland was the Deep South, and I was not sure I would like Texas Tech University. Second, as a young man I thought there was no way I would get any work done in Hawaii, so that left UMASS and that is where I headed. Again I was very lucky. Neither I nor my parents could afford a car with which I could get to Amherst, Massachusetts. However, Mr. and Mrs. Perlow, who owned and operated a men's clothing store and for whom I had worked throughout most of my college years, drove me to Massachusetts. I was excited about going to this exotic place. I had seen Tasmanian devils and red pandas in the zoo but never cows and goats, or corn for that matter.

I was very happy to be accepted in a graduate program, but it meant a detour since my advisor worked on mosquitoes. Dr. T. Michael Peters, in retrospect, not a well-known researcher, but without a doubt, for me an absolutely great advisor.

In his mind, where I grew up was irrelevant, and the fact that I was a street-smart but world-stupid kid from the ghetto in no way affected what he expected of me—he was the best! He did not assume I needed to be pampered because I was an ill-prepared inner city kid. I remember asking him what it took to succeed as an entomologist. And, he outrageously said, you need to have 12 publications by the time you get your PhD. What did I know? So I did it plus one, not because I was special but because that was the goal that was set for me. Obviously, I could not do it by myself, so it also taught me the complexities of collaborative research because without working on joint projects with others in the lab, I would not have ever been able to reach my goal.

When I completed my PhD, I was lucky enough to get a faculty job at Rutgers University. This is where two situations helped return me to moths and butterflies. In the Entomology Department, the vast majority of the faculty worked on mosquitoes. I did not want to be just another mosquito researcher. Second, at the time, an invasive species, the gypsy moth, was moving south into New Jersey. Thus, I had an opportunity to work with this moth and hopefully help mitigate the potential damage of this pest or slow its spread. Gypsy moths affect different plant species to varying degrees. I reasoned that if I could get specific information about the severity of harm to different tree species, I could estimate likely levels of damage and predict which sites or areas were more likely to experience a severe outbreak of this pest. My studies revealed that secondary plant compounds, among other things, played a role in the rate of development, size, and reproductive potential of the insects that feed on them. Secondary plant compounds include chemicals that defend against herbivory.

Thus, I began to work with other plants, as model systems such as tobacco, in order to investigate how defensive chemical compounds, in this case nicotine, affected the insects that feed on tobacco as well as the parasitoids that attack these insects. That was the beginning of a 39-year career as a professor working on the biology and ecology of moths. In particular, I focused on the theoretical and applied ecology of plant–insect interactions with an emphasis on tri-trophic level interactions. The latter entails investigating how plants directly or indirectly affect both the insects that feed on plants (i.e., herbivores) and also the natural enemies that attack the herbivores. On the applied end of things, I was interested in how these interactions influenced or enhanced conservation biological control or natural biological control.

My most recent research, prior to my retirement, illustrated this type of interaction. I explored the factors that explain the abundance and diversity (Fig. 2.3) of Lepidopteran species on trees. I investigated how plants, such as the two tree species, *Acer negundo* L. (box elder) and *Salix nigra* (Marsh) (black willow) (found in northeastern riparian forests and on which caterpillars feed), can influence parasitoid–host interactions. The tree species were selected because although both occur in the same habitat, they differ in significant ways. I examined the caterpillars that occurred on the two tree species and found that the tree species on which caterpillars feed affect their susceptibility to parasitism. I found that the level of parasitism

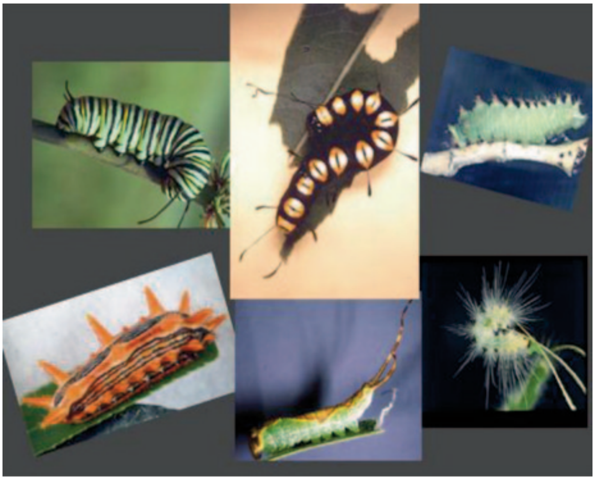


Fig. 2.3 The wonderful diversity and amazing intricacies of the caterpillars of Lepidoptera

of caterpillars on one tree species was double that of the same caterpillars on the other tree species, even among species that occur on both tree species.

The question of what was leading to these different levels of susceptibility led to a research project on insect immune systems conducted by one of my graduate students, Dr. J. Gwen Schlichta. She used a technique to study the mechanism of a caterpillar's defense against parasitism. A glass bead dyed red, representing the egg of a parasitoid, was injected into caterpillars. The "egg" was then surrounded by blood cells which formed a capsule. Once encapsulated, a real egg would die. This process differed depending on the tree species on which caterpillars occurred, suggesting that tree leaves consumed by caterpillars may contain a chemical which affects the caterpillar's ability to defend against a parasitoid.

I end this biographical sketch by emphasizing that even if one neither gets lost in remote forests nor is abducted by rebels, or some other exciting adventure, the concrete jungles of Spanish Harlem (and any other urban and suburban areas) have their own challenges for a caterpillar lover. I think that my experiences in less than pristine urban and suburban habitats led me to working in northeastern woodlands, later in my career. I was motivated by a desire to let others understand that the concrete jungle of urban and suburban habitats may not be the Amazon, but the green areas in those areas are home to amazing butterflies and moths, as well. More important is the opportunity that my life's love of insects provided me to make a difference in the lives of my students. I have loved working with students. For each student, my role evolved from an advisor teaching how science is "done," to occasional therapist, to a friend. I have learned and have always been amazed at the impact one has on students. It sometimes is difficult to realize that students really take what one says to heart. For example, one time I was taking a walk and chatting with one of my students at a meeting and he said "remember at that meeting in Toronto; we were walking outside and you said …" I thought to myself, wow! How did he remember that, it was years ago! That is when I realized students remember everything. It really illustrated to me that I really did have an impact, and I was honored.

I have always believed that one's world is only as small as you make it. So, the idea of being a generalist has always been the ideal objective. So other than my love of moths and butterflies, I love collecting masks from many cultures, which to me is the ultimate in being a generalist and appreciating a diverse and challenging world. So, I have developed a love of masks as a window into the cultures of this world. After many years I now have masks from Mexico, New Guinea, and Central and South America, as well as Africa. It is fascinating to me how masks are parts of social rituals of so many cultures and play such significant roles in these societies. But I have to admit that I cannot leave my love of insects completely behind so I also like to take pictures of, yeah you guessed it, caterpillars.

I also enjoy bronze casting and developing multimedia art pieces. My love of art is driven by a quote I once heard, attributed to Arthur M. Sackler, who presumably said, "Science is a discipline done with passion, and Art is a passion done with discipline." Although I retired in 2010, I am still writing books and working with students. I have been very lucky to have interacted with, and worked with over 100 undergraduates, and many, many graduate students, and postdocs; perhaps because I cannot imagine life without entomology. It is wonderful to find one's passion and go for it, surrounded by great people with the same passion, or those whose fledgling passion for insects and biology in general can be supported and expanded. Finally, I also love spending time with Gail, our grown children, and our six grandchildren. Who knew where a love of moths and butterflies would lead.

Prof. Pedro Barbosa PhD grew up in New York City, and after completing his BS in biology at the City College of New York, he went to the University of Massachusetts for his masters degree in the Department of Entomology and stayed there to complete his PhD. When he completed his PhD, he took a faculty position in the Department of Entomology and Economic Zoology at Rutgers University and stayed there for 2 years. In 1973, he returned to the Department of Entomology at the University of Massachusetts as an assistant professor and became an associate professor in 1978. In 1979, he took a position as an associate professor in the Department of Entomology at the University of Maryland and became a full professor in 1982. Pedro retired in 2010 and is currently an emeritus professor.

Chapter 3
Follow the Breadcrumb Trail

Carla M. Penz

Ó grande tempo
O que é meu está guardado
Não está grudado no céu
nem colado no futuro
Só sei que contigo está seguro
Excerpt from Grande tempo, by Fatima Guedes

Porto Alegre was already a big city when I was born in 1961. Some time before my parents' wedding, my grandmother Morena (née Adelina) had her house remodeled into an upstairs–downstairs duplex, and the upper floor was designed for the newlyweds. She also had the entire backyard paved with a mosaic of uneven pieces of tricolored ceramic tiles. According to my mother Isolde, grandma was tired of the "dirt" that was dragged into the house under everybody's shoes. A few planters were left along the walls to house *Sansevieria, Asparagus,* and a *Rhapis* clump. Introduced European house sparrows roosted on a tall *Dracaena* that was fragrant at night when in bloom. Grandma also had a few large concrete planters cast to resemble tree trunks where *Anthurium* plants grew. From our house, the distant noise of a sawmill could be heard all day, and there was also the hustle and bustle of a Volkswagen car dealership located across the street. How could a biologist emerge from such an urban place?

At the top of an annex at the back of the property was a large trellis-enclosed patio where my father Rubem grew orchids. He had more than 200 plants up there (easily), all well tended and pampered. One of my jobs was to collect and wash the aluminum caps that were on glass milk bottles, which I would smooth out into neat labels with my thumbnail. My father wrote on them with a dull-tipped pencil to make intaglios containing names and numbers, which he gently wrapped around a pseudobulb of each plant. Every winter the whole structure was covered with thick transparent plastic, so it was warm and humid inside when the sun was high. The

C. M. Penz (✉)
University of New Orleans, New Orleans, Louisiana
e-mail: cpenz@uno.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_3

Fig. 3.1 In the backyard of my grandmother Clara's house, posing for a picture around my uncle's Vespa motor scooter. From *left* to *right*: myself holding a plant, my brother Rubem "Mano" Penz, cousin Paulo Henrique Seth, and sister Cristina Penz. Photo by my uncle, João Batista "Tito" Freitas

orchidarium was a place of quiet solitude for my father and for me too. I remember being there until dusk one day, when lights came on in our kitchen and in those of other houses announcing dinner time. I was about 5 years old. With my hand on the green-painted metal rail, I slowly moved down the stairs smelling the air, hearing distant noises, noticing that Venus was starting to glisten in the sky. I was overtaken by a sentiment that is vivid to this day: the absolute happiness of a perfect life. Our family, our house, the plants, the fact that I could read, the subject matters I learned in school and understood, and a deep sense of gratitude for all the good things that had happened thus far. I felt fortunate and prepared—and I knew people who were not that way. At that moment I stepped out of my childhood universe to contemplate societal life and my incipient role in it.

Of course I was a regular kid and played like one, particularly because every weekend we visited my maternal grandmother Clara who had a fantastic yard where ornamental flowers and edible plants intermingled. There were fruit trees; a swing, a ditch filled with tadpoles; a soccer ball; and plenty of space for my siblings, our cousins, and myself to get dirty, sweaty, and tired (Fig. 3.1). We children were shown how to cut internodes of elephant grass to make straws to blow soap bubbles (a lesson in plant anatomy, in retrospect). Back in our orchid refuge, my father was experimenting with hybridization, and by 4th grade I was helping with that and waiting for pods to mature—which took an eternity but eventually yielded seeds that looked gorgeous under my father's miniature microscope. Seed germination and plantule development were also too slow for a child's energy level, so I kept busy with other things, such as growing mosquitoes from larvae to feed *Drosera* plants collected during summer vacations at the shore. As a back-to-school gift, my

Fig. 3.2 Type specimen of *Papilio pyrrha* Fabricius, 1775 (Natural History Museum, London). *Actinote* is the first butterfly group I studied. The photograph of this historical, weathered specimen was kindly sent to me by Phil Ackery in 1982

father bought me a copy of Mario Guimarães Ferri's[1] *Botânica, morfologia externa das plantas,* and although the pages were filled with information too advanced for a 9-year-old, the comparative morphology illustrations were amazing, and I spent hours studying them. Using my book, I identified one of his plants, *Platycerium alcicorne,* to his great delight. Incidentally, that was one of the textbooks used in my first botany class at the university (and I still have it). My path had already been set, but it took me until 8th grade to approach my science teacher to say that I wanted to be a biologist and teach classes—like him. No, you should not aim to teach in a school, he said, research is what you want to do. As it turned out, I have done both.

Upon the start of my undergraduate program in biology in 1980, I naturally gravitated towards botany, while my friends joined the zoology crowd. The botany department was limping at the time: A highly esteemed systematics professor had taken health leave, a plant ecologist was in Germany for her PhD, and other professors seemed overworked. Serendipitously, as part of his genetics class, Aldo Araújo[2] took students to the field and showed us Müllerian mimics, *Heliconius* eggs on tendrils, lycaenids with false heads, silver markings on *Agraulis vanillae,* and other incredible natural history offerings. I was instantly hooked and started an internship in the natural history museum at my old high school in 1981. Thanks to the entomologist Jesuit Father Pio Buck S. J.[3], Museu Anchieta housed the best butterfly collection in town. Aldo supervised my bachelor's thesis on the genus *Actinote* (Fig. 3.2)—my own choice of research project prompted by finding a drawer of unidentified specimens (pure zoology, despite my association with the genetics department). This work was my initiation into systematics and comparative morphology. Jocélia Grazia[4] (a Heteroptera systematist) verbally explained how to dissect

[1] Mario Guimarães Ferri: Brazilian passionate botanist, pioneer ecologist, and gifted artist. Guimarães Ferri was a professor at Universidade de São Paulo.

[2] Aldo Araújo: Brazilian geneticist, also interested in science history. Araújo initiated a new era of butterfly research in Southern Brazil by teaching us to focus on evolution and natural history.

[3] Father Pio Buck S. J.: Swiss immigrant. Father Pio was the director of Museu Anchieta, where he developed a regional insect collection. He was also a close collaborator with botanists from a local Jesuit university.

[4] Jocélia Grazia: Brazilian entomologist, who works on Heteroptera and true bugs in the family Pentatomidae in particular. Grazia was a true mentor to many students, myself included.

male and female genitalia, and back at the museum, I put her words into practice. Through her guidance I became familiar with the work of Alexander Klots[5], Karl Jordan[6], Howard Hinton[7], and other amazing entomologists of the past. At that time, to earn a bachelor's degree in genetics, students were required to take eight courses in that area of concentration. In seven of those courses, I learned about, and read works by, the usual suspects Charles Darwin[8], Henry Walter Bates[9], Alfred Russell Wallace[10], and also the more recent (but still classics) J. B. S. Haldane[11], Ronald Fisher[12], G. Ledyard Stebbins[13], George G. Simpson[14], Ernst Mayr[15], and Verne Grant[16]. In other words, my peers and I were committed to studying hard and learned English simultaneously. That was also the time when I met Keith Brown[17] (he came to visit my alma mater) and read papers by and corresponded with Woody Benson[18],

---

[5] Alexander Klots: American lepidopterist, well known by his field guides to the butterflies of North America.

[6] Karl Jordan: German entomologist, who worked with Walter Rothschild and specialized on Lepidoptera, Coleoptera, and Siphonaptera.

[7] Howard Hinton: British entomologist, who worked on many groups but was fascinated by beetles. Hinton was a gifted morphologist and an early proponent of continental drift.

[8] Charles Darwin: British naturalist, whose work was a paradigm shift in biology. His voyages and interactions with other researchers led to the proposal of natural selection as a mechanism of evolutionary change, among many other important contributions.

[9] Henry Walter Bates: British naturalist and explorer. Bates travelled through the Amazon forest and described mimicry in butterflies among many other natural history accounts.

[10] Alfred Russell Wallace: British naturalist and explorer. Wallace's voyages through the Amazon and the Malay Archipelago allowed him to conceptualize natural selection independently from Darwin.

[11] J. B. S. Haldane: British-born Indian naturalized evolutionary biologist. Haldane developed both statistical methods and theoretical models still in use today.

[12] Ronald Fisher: British statistician and evolutionary biologist. Fisher's contributions to statistics have been used in all fields of science (e.g., analysis of variance) and he spearheaded the modern evolutionary synthesis along with Haldane, Stebbins, and Simpson, among others.

[13] G. Ledyard Stebbins: American botanist and geneticist. His integrative studies of plants were groundbreaking. Stebbins helped develop the modern evolutionary synthesis.

[14] George G. Simpson: American paleontologist, who was influential in the development of the modern evolutionary synthesis. Simpson was an expert on mammals and their global distribution.

[15] Ernst Mayr: German/American ornithologist and evolutionary biologist. Mayr expanded and popularized Theodosius Dobzhansky's biological species concept and pioneered studies of speciation.

[16] Verne Grant: American botanist. He made important contributions to pollination ecology, plant genetics, and evolutionary theory.

[17] Keith Brown: American/Brazilian chemist and self-taught butterfly biologist. Brown is famous for his studies of heliconiine and ithomiine butterflies. He greatly influenced the study of butterfly biology in Brazil.

[18] Woody Benson: American/Brazilian butterfly biologist. Benson's evolutionary approach to butterfly biology and species interactions (e.g., mimicry) is internationally recognized.

João Vaconcellos Neto[19], Dick Vane-Wright[20] and Phil Ackery[21], Olaf Mielke[22], and Mirna Casagrande[23] (all of whom I met years later). But an eighth genetics class needed to fulfill my degree requirements was not available, so I took Miriam Becker's[24] *Population Ecology* instead, and she used Richard Southwood's[25] *Ecological Methods* as the text. That course was a revelation to me and filled a big gap in my background. Although this is a good summary of my formative academic years, it is also significant to place them within a socioeconomic context. The military dictatorship was starting to weaken in Brazil, but there were still "rats" (government informers) among students at the university. Repression and censorship restrained Brazilian artists, especially poets and musicians, and many went into exile abroad. Several songs I heard in my youth, and memorized for life, are rich in obscure metaphors that disguised their real intent: to criticize the military government. The economy was fragile, inflation was a serious problem, and taxes on imported science books could be as high as 80 %—my gratitude goes to professors who shared important books with us students. Interlibrary loan services could be used to obtain research papers, but that was costly, and it took 2 weeks to 1 month for requests to be filled. In those days none of us would have made it through the undergraduate or graduate programs without the invaluable service of Xerox machines and their operators, not to mention numerous copyright infringements.

Going to graduate school was a given for my closest peers and myself. This was a time in which personal decisions had professional consequences. I wanted to go to Universidade Estadual de Campinas and work with Keith Brown, but romance kept me in Southern Brazil. In 1985 I married my university boyfriend, Roberto Reis[26], a fish systematist. Aldo Araújo accepted me as a master's student and suggested a research project on the inheritance pattern of two sex-limited mimetic color forms of *Papilio hectorides* (currently *Heraclides*). Real genetics! I did not waste time, read as much as I could, and wrote Sir Cyril Clarke[27] about the project, who

---

[19] João Vasconcellos Neto: Brazilian biologist, who works on the ecology of insect–plant interactions.

[20] Dick Vane-Wright: British butterfly biologist. Dick has published on numerous aspects of butterfly biology, from systematics to mimicry. He continues to be active in the field.

[21] Phil Ackery: British butterfly biologist. Phil worked at the Natural History Museum where he developed his classification of butterflies and their host plants in addition to helping every researcher who needed access to the collection.

[22] Olaf Mielke: Brazilian butterfly taxonomist. Mielke has published on several groups of Lepidoptera and specializes on skippers.

[23] Mirna Casagrande: Brazilian butterfly taxonomist. Casagrande's work mostly focuses on taxonomy and natural history of Brassolini.

[24] Miriam Becker: Brazilian ecologist who worked at Universidade Federal do Rio Grande do Sul.

[25] Richard Southwood: British ecologist and zoologist. His influential work focused on population and community ecology.

[26] Roberto Reis: fish systematist. Reis' research focuses mostly on catfishes, and he is a professor at Pontifícia Universidade Católica do Rio Grande do Sul.

[27] Cyril Clarke: British physician, lepidopterist, and geneticist. Together with Philip Sheppard, he pioneered genetics studies of Papilionid butterflies and the peppered moth.

promptly sent me an aerogram with good advice and a few hypotheses on the genetics of the *hectorides* color forms (for youngsters: here "promptly" refers to ca. 1 month between mailing a letter and receiving a response). After 2 years of juggling with diapausing and nondiapausing pupae that were reared side by side as larvae, hand-pairing adults, and doing my best to persuade females to lay eggs in captivity (which was rather tricky), a virus killed all my larvae in 1 week. That nearly got me out of graduate school altogether, and I felt despondent enough to question my career choice. It is odd to recount the big "die-out event" somewhat dispassionately here, given that it felt quite the opposite at the time. I knew the four local *hectorides* host plants from 2 years of field observations, and my fallback project therefore asked whether oviposition preference in the field matched larval development in the lab. It did not. That was the work I presented at the 1988 Simpósio Internacional de Ecologia Evolutiva de Herbívoros Tropicais organized by Thomas Lewinsohn[28] in Campinas, where I met Thomas, Larry Gilbert[29], Bob Marquis[30], Mark Scriber[31], Lissy Coley[32], Doug Futuyma[33], and many others. Larry was recruiting students and asked if I would be interested in doing a PhD in his lab. It was an exciting opportunity, so I applied for and was granted a graduate fellowship through a Brazilian funding agency (only four were given to zoology in the entire country, so my hard work paid off). I moved to Austin, Texas, in the August of 1989 with two suitcases of essentials, leaving everything else behind.

The first semester at the University of Texas (UT) was intense in all respects—classes, reading assignments, working on the manuscript from my M.S. research, hanging out with Mike Singer[34] and his lab members, and meeting so many people—it is hard to remember them all. I was not prepared for such a marathon, and considering my previous standards, I did poorly that semester. Dealing with all aspects of life in a foreign language took a lot of energy—I remember how hard it was to listen to the lecture and take notes at the same time. Speaking on the phone was surprisingly difficult (no body language to aid communication). Nonetheless, being

[28] Thomas Lewinsohn: Brazilian ecologist. His research initially focused on insect–plant interactions but now also encompasses community diversity and conservation.

[29] Larry Gilbert: American butterfly biologist. Gilbert's research on *Heliconius* butterflies spans the fields of ecology, evolution, and genetics.

[30] Bob Marquis: American evolutionary ecologist. Marquis' research focuses on tritrophic interactions of plant–herbivore systems and the ecology of plant resistance against herbivores.

[31] Mark Scriber: American butterfly ecologist. Scriber's research interests include nutritional ecology and insect–plant interactions, mechanisms of host plant resistance and insect counteradaptations, and color polymorphisms, among several other topics.

[32] Lissy Coley: American evolutionary ecologist. Coley works on the role of defenses in protecting plants from damage by herbivores and pathogens.

[33] Doug Futuyma: American evolutionary biologist. Futuyma's research ranges from insect–plant interactions to coevolution and sexual selection. His books are standards for students of evolution.

[34] Mike C. Singer: British/American butterfly behavioral ecologist. Singer's studies of host plant preferences in *Euphydryas editha* butterflies span several decades in California and constitute milestones in evolutionary ecology of insect–plant interactions.

surrounded by a fantastic group of people made a huge difference. Nancy Greig[35] was my first office mate and gave me a much-needed crash course of everyday words in English plus all sorts of other practical advice (e.g., go to the Goodwill thrift store to buy field clothes). Phil DeVries[36] and Peng Chai[37] were still at UT after finishing their PhD, and we became friends instantly due to shared scientific interests. During this time, I became involved with my lab mate Bob Srygley[38] who studied butterfly flight in collaboration with Peng. The Brazilians Evandro Oliveira[39] and Marcio Zikán Cardoso[40] joined the lab 1 year after I arrived, and Mirian Medina Hay-Roe[41] later came from Peru. We were a truly cohesive group of people who encouraged one another, collaborated in projects, and made comments and suggestions on each other's research manuscripts. Times were busy, the good kind of busy, and after my brain adjusted to a new language and faster pace, the graduate school experience became more pleasurable. For my PhD project, I decided to use comparative morphology to reconstruct a phylogeny of Neotropical Heliconiini. As a diagram that represents evolutionary history, a phylogeny provides the framework to ask biological questions about a particular group. For example, are the oldest heliconiine lineages associated with the oldest *Passiflora* host plant lineages? Phylogenies of butterflies and plants are required to answer questions such as this. Larry was a tad disappointed with my choice of data (morphology) because systematists were starting to use deoxyribonucleic acid (DNA) sequencing for phylogenetic analyses, and he thought I should do the same. Although I learned the basics of DNA sequencing, I stayed with comparative morphology because handling and dissecting specimens is the type of work best suited for me—a visual person fascinated with anatomical complexity. When placed in an evolutionary context, the study of morphological diversification encapsulates Darwin's concept of *descent with modification*—diversification in structure from ancestral to descendant life forms. This is what drove me to comparative morphology, and I will

[35] Nancy Greig: American biologist. Greig is the director of the Cockrell Butterfly Center at the Houston Museum of Natural Science.

[36] Phil DeVries: American butterfly biologist and ecologist. Phil is a keen and eclectic field naturalist. He is best known for his work on butterflies of Costa Rica, symbiotic associations between riodinid caterpillars and ants, and the community diversity studies of fruit-feeding butterflies.

[37] Peng Chai: Chinese/American biologist. Currently senior biostatistician at MDS Pharma Services, Lincoln, NE. Peng's butterfly palatability experiments and flight morphology studies are a landmark in butterfly biology.

[38] Bob Srygley: American biologist, who worked on butterfly flight and migration in Panama. Srygley is a research scientist at the United States Department of Agriculture (USDA) working on Mormon cricket and grasshopper management in addition to butterflies.

[39] Evandro Gama de Oliveira: Brazilian butterfly biologist, who worked on butterfly flight and migration in Brazil and Panama. Oliveira's research also includes community ecology of fruit-feeding butterflies.

[40] Marcio Zikán Cardoso: Brazilian butterfly biologist whose research focuses on the evolutionary ecology of *Heliconius* butterflies.

[41] Mirian Medina Hay-Roe: Peruvian/American butterfly researcher, who works on several aspects of *Heliconius* biology at the University of Florida.

Fig. 3.3 Carla watching butterflies at the forest edge along the River Cristalino, MT Brazil (2009; Photo by Phil DeVries)

never cease to be fascinated by the sheer richness of structural and color diversity in butterflies (Fig. 3.3).

I went to Costa Rica for the first time in 1990 with Larry Gilbert's field course. It was truly refreshing to walk around the forest without the fear of being mugged or hurt (my field site in Southern Brazil was not safe). I went to Panama and Ecuador multiple times during my graduate program, and I also did fieldwork near the Brazilian Amazonian state capitals of Manaus and Belém. The main point of my trip to Manaus was to find the larvae of *Neruda aoede,* but after extensive search their host plant, *Dilkea,* was nowhere to be seen. Aloísio, one of the seasoned field-workers from Instituto Nacional de Pesquisas da Amazônia (INPA), heard that I was looking for such a plant and came to talk to me. He told me that he never found it at the site where we were, but he had tagged one *Dilkea* specimen in an inventory plot at the next bio station up the road. Aloísio gave me detailed directions to locate it: plot number, distance from the beginning of a particular transect, noting that the plant would be three paces from the transect edge—to the right. He apologized for not remembering the specimen number but assured me that the plant was tagged. Luckily, I was offered a car ride by an agronomist who listened to the whole conversation and happened to be going that way. He seemed enthused by the narrative and wanted to see this mysterious plant. When we got to the proper place, the plant was actually three paces *to the left* of the transect, and my guide for the day shook his head. I said, "No problem, we found the plant anyway, but it is too bad that there are no eggs or larvae on it." That was not his point. He said, "Aloísio never ceases to amaze me. It has been 2 years since he has set foot in this place." Life allowed me to meet many remarkable people in vastly different places….

In Panama, I was looking for heliconiine early stages for my PhD research, but also reared larvae of other groups on the side. That was the purpose of my trip to Ecuador too, and the mission was to find and rear two species: *Podotricha telesiphe* (at mid elevation) and *Neruda aoede,* which had eluded me in Manaus. In Baeza (1500 m), I found *Podotricha* eggs almost by accident because they are nearly identical in size and color to those of a common josiine moth that oviposits on the same *Passiflora* host. *Podotricha* eggs are striated though, and they look opaque when you flip the host plant leaf (the moth eggs are smooth and slightly shiny). It takes about 2 months for *Podotricha* to develop from egg to adult, so I practically became part of the family I stayed with in Baeza and was even dragged to mass every weekend by Doña Teresita, the owner of the hotel El Nogal de Jumandi. Instead of glass, the window of my hotel room was covered with plastic sheets that barely kept out the cold evening breeze, but the thick wool blankets were cozy and warm. Across the street from the hotel was Restaurante Gina, where I stopped for a cup of coffee and a *Manicho* cholocate bar with peanuts every day after fieldwork. People in Baeza were surprisingly familiar with transient researchers, especially botanists and butterfly biologists, and they showed me important landmarks (remnants of a stone-paved colonial times trail) and folk remedies (wax of a fulgorid nymph used to treat infected wounds). During the same trip, in my first walk through the lowland forest at Jatun Sacha Biological Station, I found a cluster of *Neruda aoede* eggs on a new shoot of *Dilkea* just a meter off the ground and right in the middle of a trail! As far as I know, Rev. Arthur Miles-Moss[42] had been the only other person to rear that species some 80 years before. Although *Podotricha telesiphe* and *Neruda aoede* are the two most remarkable caterpillars I have reared, every single species has been a gift. I could write pages and more pages about what happened during my 3 months of fieldwork in Ecuador in 1992, but these two short accounts provide a good depiction of how things went.

I had the opportunity to live in England for 1 year in 1993. During that time, I spent 1 day per month at the British Museum of Natural History and will never forget that Phil Ackery always came to chat at about midmorning, two cups of coffee in hand. It was a privilege to get to know Phil, learn from him, and to examine specimens collected by Bates and other heroes of mine. I also met Dick Vane-Wright, Miriam Rothschild[43] (Phil introduced us!), Bernard d'Abrera[44], Jim Mallet[45] and Sandy Knapp[46] plus their children, and reconnected with George Beccaloni[47] (who I had met at Jatun Sacha the previous year). Comparative morphology, phylogenetic systematics, butterfly behavior, evolution, and general biology were definitely at the very center of my life, and that was also the case for most of my friends and new acquaintances. The year in England was truly productive and opened new horizons for me, but it went by fast. It was time to return to my home base in Texas to finish my PhD project.

---

[42] Rev. Arthur Miles-Moss: British vicar, artist, and amateur lepidopterist. His Parish spanned the Brazilian Amazon, which allowed him to travel throughout the region collecting and rearing butterflies.

[43] Miriam Rothschild: British amateur entomologist. Rothschild was an accomplished expert on fleas and made important contributions to the study of chemical ecology of Lepidoptera.

[44] Bernard d'Abrera: Australian amateur lepidopterist. d'Abrera is best known for his series of volumes on the butterfly fauna of the world.

[45] Jim Mallet: butterfly evolutionary biologist. Mallet's research focuses on *Heliconius* mimicry complexes.

[46] Sandy Knapp: American botanist. Knapp is a specialist on the family Solanaceae, especially in the Neotropics.

[47] George Beccaloni: British entomologist. Beccaloni studied Neotropical ithomiine butterflies for his PhD but now focuses on his real passion: cockroaches.

Not butterflies but a long-standing friendship brought Phil DeVries and me together, and we were married in 1997. In my opinion, however, there is no relationship more complete than that between two people who share intellectual passions. Indeed, individually and as a couple we have been criticized by family and friends for "doing nothing but work" (which is not exactly true). We both recognize that there is no line between our personal lives and our research, and Phil has been my greatest supporter, critic, and idea partner—with an occasional hint of aggravation to keep things interesting. It was during our partnership that my research approach matured and became more integrative.

When in Phil's lab at the University of Oregon, I started to work on the main manuscript from my PhD dissertation—the phylogeny of Heliconiini. When the study was finally published in 1999, I was excited to send out reprints to potentially interested colleagues. The list of recipients included Lt. Col. John Eliot[48], who replied with compliments, comments, and quite a few questions. We began what would become a regular correspondence, and John asked me to explain the basic principles of cladistic analyses, which I did. He replied with insightful remarks such as "not all structures have the same importance" and, of course, more questions. We continued to exchange letters even after Phil and I moved to Wisconsin to work at the Milwaukee Public Museum. At some point, I was late replying to one of John's letters due to a ridiculous amount of time devoted to a grant proposal. He sent me an aerogram explaining his urgency—he was dying of cancer. Needless to say, I wrote immediately with an apology, the answers, and sincere sorrow for what was inevitably happening to him. John responded that he was at peace with the circumstances (in fact he addressed *me* with comforting words). He thanked me for the information, which was needed for his final revision of Corbet and Pendlebury's *The Butterflies of the Malay Peninsula*. That was my last exchange with Lt. Col. John Eliot—a true gentleman—whom I never met in person, but felt in spirit.

In 2002 my first research project on *Morpho* butterflies was published, the largest and most celebrated butterflies I had ever studied. Exploring closely related groups seemed a natural course of action, and I started to look into brassolines and amathusiines, making good use of museum collections. This is the perfect place in my narrative to acknowledge field biologists for their efforts collecting specimens and museums for safekeeping and making them available to the research community. Without collections I could not do the work I do and definitely would not have become the person I am.

Phil and I moved to Louisiana to join the faculty at the University of New Orleans in 2004 (1 year before the infamous hurricane Katrina), where I continue to expand the research projects started long before. I gave a seminar about my work in Copenhagen early in 2005, when I had the honor to meet Niels Kristensen[49], his

---

[48] Lt. Col. John Eliot: British amateur lepidopterist, specialist in Oriental butterflies, and editor of Corbet and Pendlebury's *The Butterflies of the Malay Peninsula*.

[49] Niels Kristensen: Danish comparative morphologist and systematist. Kristensen's knowledge of structure and function spans the entire order Lepidoptera.

former PhD student Thomas Simonsen[50], and several other researchers. Timidly, I showed Niels a series of riodinid male genitalia drawings demonstrating that homologous anatomical parts had become fused in different ways along the diversification of the group. He smiled at the illustrations in genuine interest saying that the repeated evolution of such patterns within Lepidoptera never ceased to amaze him. Niels' words made my heart sing, given that they came from one of the most knowledgeable researchers in the field who has directly or indirectly touched the lives of all contemporary comparative morphologists working with Lepidoptera. It is always a pleasure to receive and read his publications, many of which are much broader in scope than what most researchers could ever hope to accomplish, myself included. For practical reasons, my work has become more focused, and during the past 15 years, Neotropical brassoline butterflies have been extremely generous to me. I have studied their morphology, phylogeny, and wing color variation at the tribal and generic levels. Diversification of projects is usually correlated with collaborative work with colleagues (old and new), and Phil and I have joined forces with good friends such as George Austin[51], Niklas Wahlberg[52], Russ Lande[53], and André V. L. Freitas[54]. After all, collaborative research allows each collaborator to do what we do best. Thank you George for being passionately obsessed with butterflies and sharing information and specimens; Niklas, for choosing DNA sequence as your preferred data source; Russ, for knowing a lot about numbers and just enough about butterfly biology; and André, for being a strong supporter of butterfly research in Brazil.

What about here and now? I feel my main research field for so many years, phylogenetic systematics, may not be enough to drive me forward. My career path seems to be doing a full circle back to natural history, which provided the original impetus to study butterflies. I will forever be in awe of their immense morphological and evolutionary diversification—a surprise in every dissection, every field observation, and every group. Butterflies are magnificent living sculptures that allow me to do creative work. They make me think and keep me awake at night (in a good way). Professional commitments and distance to Neotropical forests are making it

[50] Thomas Simonsen: Danish comparative morphologist and systematist. Simonsen was Niels Kristensen's student and has worked on both butterflies and moths.

[51] George Austin: American lepidopterist. Austin collected butterflies throughout the Neotropics, was thoroughly dedicated to collection organization and curation, and did transect counts in his own backyard every weekend. He was the foremost North American authority on Neotropical Hesperiidae.

[52] Niklas Wahlberg: Finnish butterfly systematist. Wahlberg pioneered modern phylogenetic studies of Nymphalid butterflies using deoxyribonucleic acid (DNA) sequence data. He is also interested in evolutionary diversification and biogeography of Lepidoptera in general.

[53] Russ Lande: American evolutionary biologist. Lande's work spans quantitative genetics, evolutionary mechanisms (genetic drift, selection), speciation, and phenotypic plasticity. He also works on community diversity in collaboration with Phil DeVries and other researchers.

[54] André V. L. Freitas: Brazilian butterfly biologist. Freitas was a student of Keith Brown. He is a prolific researcher, who has worked on the systematics and natural history of several Neotropical groups.

difficult for me to spend extended periods of time in the field, and as a result I have become even more aware of the importance of making rigorous and reliable field observations. Natural history observations provide the spark for everything else we seek to learn through either classical or advanced technological means. No matter how small, each of our (collective) butterfly studies brings us closer to the natural world—and that is the reason why I became a biologist. Academia has changed tremendously since many of us started our careers, and natural history museums seem to be at risk of extinction. So, I do think about the day when I may not be able to perform my work in a way that meets my own standards and satisfaction. That will not be tragic, but merely the conclusion of a fantastic journey that can be retraced by following the breadcrumb trail of my publications. My work is my history and my legacy.

Carla M. Penz has had an interest in biology from childhood and started to study butterflies as an undergraduate intern at Museu Anchieta in Brazil. She obtained her bachelor and master of science degrees at Universidade Federal do Rio Grande do Sul and her doctorate at the University of Texas at Austin. During that period she travelled to Costa Rica, Panama, Ecuador, and Brazil for fieldwork and more recently to South Africa and Peninsular Malaysia. She has also spent time in England as a visiting researcher at Cambridge University and the Natural History Museum. Carla worked as a curator of Lepidoptera (2000–2004) and Section Head of Invertebrate Zoology (2003–2004) at the Milwaukee Public Museum. She is currently an associate professor at the University of New Orleans (2004–present) and a research associate of the American Museum of Natural History, Milwaukee Public Museum, and Pontifícia Universidade Católica do Rio Grande do Sul. Her research focuses on two butterfly families, the Nymphalidae and Riodinidae. Given her broad interests, she has published research papers on various aspects of their biology, including comparative morphology, phylogenetics, feeding and mating behavior, and larval biology and morphology—all within the context of evolution. In particular, her work on comparative morphology of the Brassolini (owl butterflies) and Riodinidae (metalmarks) is the most detailed ever performed for these butterflies and sets new standards for research into their systematics. Carla is a proud gaúcha from Porto Alegre, where she goes every year to visit her family. She nourishes her inner self by listening to Brazilian music, playing percussion instruments, dancing, cooking, sewing, reading, and fondly watching the intellectual growth of her nephew and nieces.

Part II
Adventure

There's no need to build a labyrinth when the entire universe is one.
Jorge Luis Borges, *The Aleph*

I do not know if this is true of other fields of science, but the biological sciences value travel and physical exploration. Perhaps this is because we are children of Darwin and Wallace and their journeys, or perhaps it is because we are optimists and always want to study subjects that are worth the trip. Or could it be that the possibility of real adventure, in the dangerous sense, is a part of the scientific process that does not get covered in text books? I do not have an answer for that, but I would guess that the authors of these next chapters just might.

MLF

Caterpillar and vegetation. Illustration by Su'ad Yoon

Chapter 4
Contingency

Art Shapiro

Life can only be understood backwards; but it must be lived forwards.
Soren Kierkegaard

It all goes back to the early 1960s, I guess.

I was an undergrad at the University of Pennsylvania, nominally majoring in biology but in fact majoring in extracurricular activities—which included journalism *(The Daily Pennsylvanian)*, student activism, and studying butterflies. I took a BA, not a BS, and satisfied my language requirement with French, which I had pursued in high school. Not that I had any concept of potential future utility for my French; it was just the path of least resistance. And it fed into the philosophical preoccupations of the day. After all, Jean-Paul Sartre was French, n'est-ce pas?

And I took a course in the French Revolution, too.

I had no particular interest in Latin America per se. As a Philadelphian, the only "Latin Americans" I had ever interacted with were Puerto Ricans. But I did have an interest in revolution and revolutionaries, and I found myself taking an upper-division course in Latin American politics, taught by Dr. Henry Wells. Dr. Wells was very surprised to have a bio major in the class and even more surprised when I aced it. He was an expert on the Dominican Republic, and he told us the convoluted story of developments there after the fall of the Trujillo dictatorship, and how in the world of politics contingency ruled—one was always being overtaken by events. That, and a lot of the substantive content of the course, stayed with me. But as with French, I saw no potential utility in knowing about the unique historical-political trajectories of the Latin American republics—why every one of them was different from the others.

Meanwhile, I embarked on a project to do a butterfly fauna of the Tinicum Marshes near Philadelphia International Airport. I went there once a week and

A. Shapiro (✉)
University of California, Davis, USA
e-mail: theochila@gmail.com

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_4

recorded what was flying. I took a course in community ecology from Dr. Jack McCormick. He had a joint appointment between Penn (where the great environmentalist-landscape designer Ian McHarg had hired him as vegetation ecologist in the Landscape Architecture Program) and the Philadelphia Academy of Natural Sciences. As an old hand in the New Jersey Pine Barrens, I acted as a teaching assistant on McCormick's field trips there. (He himself had studied pine barrens ecology under the great forest ecologist Murray Buell.) The academy had a field station in suburban Devon, along the commuter rail main line, where McCormick was doing highly innovative studies of the mechanisms of old-field succession. He hired me as a summer field-crew member at Devon. While working there, I saw what may have been the last regal fritillary *(Speyeria idalia)* seen in Pennsylvania in the twentieth century. McCormick got my Tinicum report published as an appendix to a study prepared for the Conservation Foundation. I had no idea then that it would serve as a template for one of the two centerpieces of my career. That was just one more thing I had no idea about. The rest of this essay is about the *other* centerpiece.

The Biology Department at Penn had a genial old entomologist. His name was Rudi Schmieder. It was painfully obvious that the rest of the faculty viewed him as a quaint anachronism *(an entomologist in an Ivy League Biology Department in 1963?)* and could barely wait for him to retire so they could hire someone at the proverbial cutting edge. Rudi taught a sparsely enrolled entomology course, which he assured me I had no need to take because I already knew everything in it. He did teach me how to dissect genitalia, which skill I honed on a series of unlucky *Orthosia hibisci* (a very abundant late-winter noctuid moth). The male genitalia of many insects, including Lepidoptera, are exceedingly useful for doing species-level taxonomy, and knowing how to handle them is an essential part of a lepidopterist's education. Rudi retired in my senior year. He told me that in his entire career at Penn, he had had only two students who truly loved insects—Paul Ehrlich and me. Paul wasn't around, but I was, and when Rudi cleaned out his office, he presented me with essentially all his separates (reprints of published works, which were distributed by the authors by mail in those long-ago days before PDFs existed) on Lepidoptera, plus his entire file (including original correspondence) on Orazio Querci, an Italian commercial butterfly collector who immigrated to Philadelphia, and in the 1930s carried out primitive population dynamics studies of the checkered white, *Pontia protodice,* something Rudi knew I was myself doing then. Querci's material was unpublished. I still have his original data and notes and still think I might do something with it. Rudi also gave me a magnificent German chromolithographed volume impressively titled *Das Buch der Schmetterlinge*. Among the many papers, in various languages, were several by a Professor Jose Herrera of the University of Chile, some in English, coauthored with William D. Field, of the Smithsonian. I had actually met Field when I was in Washington, DC as a high-school senior competing in the national Westinghouse Science Talent Search. But that's another story. The Herrera and Herrera–Field stuff that intrigued me most was about South American pierids. I couldn't read Spanish, of course, but the illustrations suggested to me that at least some species of the genus *Tatochila* had seasonal phenotypes like *Pontia* did. I was already launched on experimental studies of the environmental control of seasonal polyphenism, but in the 1960s, I never seriously entertained the notion of actually working on this creature called *Tatochila*.

Lots of stuff happened after graduation, but those loose threads all kept dangling.

And then I got a paper by one Phil Ackery of the British Museum. It was now 1975. I was an assistant professor at the University of California (UC), Davis, on the threshold of tenure. I had used the Tinicum study as the basis for a monitoring project in California, initially conceived as a 5-or-so-year endeavor, which I had described in a chapter of the symposium published in memory of my late mentor at Penn, Dr. Robert MacArthur. (It was a singular honor to be invited to contribute, having been but a precocious undergrad camp follower of the master.) I was concentrating on projects close to home. The Ackery paper, published in the *Bulletin of the Allyn Museum*, described a new monotypic pierid genus and species from Colombia, *Reliquia santamarta*. It had been discovered at a place called Cambirumeina on the southeast side of the Santa Marta range, in the alpine zone, by a young Brit named Michael Adams, who for his DPhil thesis was doing the biogeography of the pronophiline satyrids of the region—he wasn't looking for a pierid; it found him. I looked at the photographs and the genitalia, and I said to myself, "*This thing is a f------ Pontia! What is it doing in Colombia*?" And in a strange part of Colombia, too: the Sierra Nevada de Santa Marta in the extreme northeastern part of the country, near the Caribbean coast, separated by a deep trough from the Andes proper and, as I learned by reading up on the place, sporting an astonishing level of endemism in almost everything. That was interesting, but what was most interesting to me was the fact that *Reliquia* duplicated the hindwing-underside pattern of the cold-season phenotypes of *Pontia*. In fact, except for its oddly long antennae, everything about it looked like *Pontia*. Even the genitalia!

I had already shown that the allegedly monophenic North American *Pieris virginiensis* could be "tricked" in the lab into producing a spotless nondiapause, summer phenotype just like its close relative, *P. "napi" oleracea.* (*P. napi oleracea* looks very different in its spring and summer generations, a condition called polyphenism. The seasonal forms are induced by the day length and temperature conditions experienced by the larva and pupa during development. But *P. virginiensis* has only one generation a year and always shows the spring phenotype—it's monophenic. Because polyphenism is closely linked to dormancy or diapause, one has to "trick" *P. virginiensis* into developing directly.) One just had to rear it under continuous light, a "nonsense" photoperiod. I had interpreted that as evidence that univoltinism/monophenism was a derivative condition in *P. virginiensis* vis-à-vis *P. "napi."* And I was thoroughly familiar with the work of the Berkeley zoologist Alden Miller on Andean sparrows, in which he demonstrated the latency of photoperiodic reactions in equatorial populations whose breeding seasonality was not tied to photoperiod in nature. He used this to infer their biogeographic history—long before phylogeography. So I had this wild idea: What if I could culture *Reliquia*, from 10° north of the equator, and rear it under a regime that would induce a spotless "summer" hindwing in *Pontia*? Would it do it? And if it did, would that tell us it really was a *Pontia*, stranded in this bizarre place perhaps as a consequence of equatorward displacement during the Pleistocene? What a delicious scenario!

I was turning 30 in 1976 and beginning to feel untrustworthy (per Abbie Hoffman)—if not actually "old." I wanted to do something macho, something off the wall. (I'd been reading a lot of William S. Burroughs.) I contacted Michael Adams, who was more than eager to assist me in my tentative project. He provided me with great detail on the locality and how to get access and put me in touch with numerous key contacts on the ground in Colombia, or at least told me how to find them (one indispensable fellow who drove a jeep taxi and knew the way to the trailhead hung out at "cinco esquinas" in downtown Valledupar—keep in mind this was long before cell phones or e-mail). I put in an application for a small grant from National Geographic, figuring they'd be turned on by the exotic locale and/or the wild-ass premise. I guess they were; I got it.

And suddenly that course in Latin American politics became useful. I was going to Latin America!

My wife, who had at least a little Spanish, as well as a botanist from the Bay Area named Art Weston, who had quite a bit, made up the rest of our expedition, and off we went in January of 1977. We were in the Sierra Nevada for 2 weeks. We made very good use of the leads and suggestions from Adams but almost came a cropper at the last minute. We needed to get a *salvoconducto* (safe-conduct pass) from the mayor of Valledupar to go legally up the mountain into Indian country. The mayor was immediately suspicious of our motives. Apparently, there had been left-wing anthropologists stirring up the Indians, and that's what he thought we were: left-wing anthropologists in disguise. A beautiful young woman in the mayor's office overheard our plight and intervened in our behalf. She closeted herself with the mayor for several minutes and then emerged with our *salvoconducto* in hand. We have no idea to this day how she got it. I learned a lot about tropical high-altitude ecology very fast. I also learned a lot about Latin America at a breakneck pace. Colombia was having a drought and was heavily dependent on hydropower. Electricity was rationed. Of course, that only affected us in town, but we got to see things at their most disorganized in a country not noted for its organization. The only electricity we had in the Sierra, of course, was from the battery in our teenage guide Gregorio's radio, which he kept tuned to the soccer matches so that the mountain fastnesses echoed with the frantic announcer's shout of "*GOL!GOL!GOL!GOL!GOLLLLLLL…*" and the magnificently-trilled l's of the ads for "*AGUARDIENTE BLANCO DEL VALLLLLLLE!*" Gregorio left us on our own after a few days. We had gone higher than he had ever been before, and he did not like the freeze-dried egg dish we ate daily and had christened "*huevos Icachui*" after the mountain that loomed above us. We saw our first *Reliquia* on the ascent toward Cambirumeina from the Mamancanaca Valley. There was no time to grab a net before it was gone. It was a female. I had a dark vision that it was to be the only female we'd see, and we had come all that way just for a moment's glance.

But we saw plenty of them once we were ensconced in Cambirumeina (Fig. 4.1).

We got *Reliquia* eggs. I inferred that the beast must eat crucifers, and it did. We got our precious cargo back down the mountain. We were officially in the Sierra Nevada as "nature photographers." We were concerned about getting our bugs out, because the *alferiz* ("sheriff") at San Sebastian de Rabago, the town at the

Fig. 4.1 Clockwise from the *upper left:* (1) Glacial Mamancanaca Valley, Colombia, looking toward the pass to Cambirumeina, where we saw our first *Reliquia*. The triangular peak is Cerro Icachui. (2) Our camp at Cambirumeina on a particularly cold, miserable afternoon. (3) Adrienne and me in camp at Cambirumeina (photo by Art Weston). (4) Chilean puna in Lauca National Park. The base is about 3800 m; the peaks rise to well over 6000 m. (5) Meeting (accidentally) with the Club Andino de Valledupar on the way down from Cambirumeina. The Ica Indian in traditional dress is the Club's chief guide

trailhead, had insisted on checking our stuff for contraband (the Sierra Nevada is full of archeological sites, and gold artifacts can be found even today). We had a fixed appointment to present ourselves at his office, but when we showed up, he was nowhere to be found. Our jeep driver was there, though, and told us to hop in. Off we went. He then told us, babes in the woods that we were, that on the assumption we *might* have some kind of contraband, he had used a percentage of what we paid him to bribe the *alferiz* to get lost.

Welcome to Latin America, kids!

Postscript: The mayor's fears about left-wing anthropologists were well founded. A few years later, the Indians expelled the Catholic missionaries, took back their town and changed its name from San Sebastian de Rabago back to the original Nabusimake. The Nicaraguan Sandinista regime published a book celebrating the event as a milestone of indigenous anticolonialism.

On we went to Cali, which we were to use as a base of operations for work in the treeless high-altitude zone *(paramo)* of the nearby Cordillera Central de los Andes. We rented a room in a private home in a middle-class neighborhood and I reared my *Reliquia* there, having convinced the lady of the house and her maid (i) never to turn off the lights and (ii) never to spray the room with pesticide, which was a routine activity otherwise. The mosquitoes ate us alive until 3 AM, when they suddenly disappeared and we could sleep—but not in the dark. The experiment required rearing under continuous light, which as I noted before, induces summer phenotypes in most pierids. Because of the drought, the electricity would be off for hours every day, so we kept a votive candle burning next to the rearing cage 24 h a day. The maid must have thought we were very devout! (One doesn't have to believe in a Deity to pray for the success of such a crazy experiment.) We in fact got nondiapausing pupae and perfectly normal adults, with no hint of phenotypic plasticity. We reared the bug on peppergrass *(Lepidium),* which I had found growing abundantly in a vacant lot next to a movie theater downtown. When we were almost done rearing, I went to harvest the host plant and found that a 10-ft brick wall had been built the day before, closing off access to the lot. We went into the theater and asked if the custodian had a ladder. Theaters always have ladders, for changing what's on the marquee. They did and let me use it. I went over the wall and gathered enough to see us through to the last prepupa. They said the wall had been built to keep the bums out. Almost worked for me!

My Spanish was improving daily, so much so that before we moved out I had an extended political argument with old Uncle Jesus, fueled by *Aguardiente Blanco del Vallllle*. I read the newspaper daily and whenever I could, I watched the soap operas—*telenovelas*—which offered a passport to vernacular speech, even if it mostly concerned adultery, pregnancy, and crime.

By the time we went home at the end of February, I was hooked on Latin America—in part because, though a first-time visitor, I actually knew a lot about Colombia beforehand from that Poli-Sci course, and what I was living made sense. We actually went to a huge political demonstration in downtown Cali, despite our landlady's warnings: "They kill people at those things!" The demo was ringed by a phalanx of teenage policemen with heavy plastic shields and semiautomatic weapons. The rhetoric was florid, and nothing untoward happened. But I was yet to encounter Argentina.

Back to those Herrera papers from Rudi! The *Tatochila* that most looked like it had a seasonal polyphenism was *T. vanvolxemii* from central Argentina. We had a few specimens in the UC Davis collection because Professor Richard Bohart (in his youth a lepidopterist, later a hymenopterist) had collected in northern and central Argentina alongside Dr. Abraham Willink of the Instituto Miguel Lillo of the National University of Tucuman. Bohart put me in touch with Willink, who was glad to help facilitate a collecting trip. My colleague Dr. Michael Barbour, a plant ecologist, had worked in Argentina during the International Biological Programme in the 1960s, when there was extensive interhemispheric collaboration, in this case on the community ecology of creosotebush deserts. Barbour had oodles of maps and literature, which he put at my disposal. Of all the countries we had studied in Dr. Wells' course, I had found Argentina the most intriguing. And now I was going there! (Figs. 4.2 and 4.3).

My wife and I went in November 1977. We were "Arturo and Adriana" from the start. The trip was a resounding success. We traveled widely in a rich array of biomes, making friends everywhere and eating some of the best food we had ever had. Argentina was ridiculously easy to get around and work in. There was only

Fig. 4.2 Catamarca: Arid high-altitude bunchgrass at 5000 m in the puna of northwestern Argentina

Fig. 4.3 *Hypsochila* female, unknown species. Jujuy, Argentina

one problem: It was under the heavy thumb of an openly fascist military dictatorship. That fact was rarely a direct problem to us, though we learned what to say and what not to say and not to do a visible double take when the news kiosk where one bought one's daily *Clarin* also exhibited the vicious magazine *Cabildo* with a photo of Mussolini on the cover, or a comic book with Nazi spies as the heroes and the Brits as villains, or a paperback called *La Derrota Mundial* ("The Global Rout"), with a battlefield on the cover, littered with burned-out tanks under a blazing red sun sporting a Star of David. (The book's premise is that the "Jewish" regime of Communist Russia conned the West into destroying Hitler—had we not fallen for the con, everything would have been utterly copacetic.)

We found it very easy to separate the people in the street from the regime, which of course inspired many nights lying in bed talking, talking, talking, pondering how such monstrosities come to power, whether in Germany or Italy or Argentina or

Chile. At this point, we began having kids, and I began going south alone. That gave me even more freedom—I had no commitments to anyone but myself and could go where and when I pleased. My Spanish had become totally Argentinized, and I could actually "pass." I began referring to Argentina as "*mi segunda Patria*" (my second homeland). I traveled the entire length of the country, "*desde La Quiaca* (on the Bolivian border) *hasta Ushuaia* (Tierra del Fuego)." Prior to the economic crisis of 1930, Argentine entomology had been on a par with America or Western Europe. But in the turbulent decades that followed, science in general went into free fall. For many years, the only person doing serious work on butterflies in Argentina was an English expat, Kenneth Hayward (based in Tucuman). As a result, when I began doing serious work on butterflies in Argentina, virtually everything I learned was new to science. And unlike Hayward, I was working not as a taxonomist or cataloguer but as an evolutionary ecologist and biogeographer: my efforts were problem-driven. The best ecologists in Argentina, like Eduardo Rapoport, who was then in Mexico City, were living in exile abroad. Fortunately, they mostly came back after the nightmare was over.

On my next trip, I crossed over into Chile and met Pepe Herrera, whose papers Rudi had given me some 20 years before. Chile was under the Pinochet dictatorship. Herrera was a moderate *Pinochetista* with military connections, so we did not talk politics—only science, with occasional discussion of the physical attributes of passing women (Pepe was an old coot, but very appreciative of *lolas*, as hotties are called in Chile). "My" pierids are numerous in the extreme north of Chile, in the arid-alpine *puna*, but become increasingly scarce in the south where the climates are cloudy, cool, and damp; there is a good fauna only in the tiny bit of the much drier Patagonian steppe on the Chilean side of the border, near Torres del Paine. So, there is less incentive for me to work there than across the Andes. And while I enjoy my time in Chile and like the people, I enjoy Argentina more. I think the reason is the strong Italian cultural strain in Argentina. On our very first trip in November 1977, as we sat in an Italian restaurant eating a splendid meal, I said to my wife "I feel like I'm back in South Philadelphia!"

Thirty-seven years of work in Latin America (a lot in Mexico and a bit in Peru, too) generate far too many stories to pack into an essay like this. That's especially true for my Argentine experiences, which literally changed my life. Working and traveling in the shadow of one of the world's most vicious governments leaves an indelible impression. Watching that regime fall and watching civil society and the arts return from underground, likewise. (The anthem of the resistance was "*Como la Cigarra*"—"Like the Cicada"—a song that celebrates the marvelous reappearance of that insect after years underground, "singing to the sun." It's a song I cannot hear without tearing up, even now, three decades later.) Talking candidly with all kinds of people in all kinds of situations, on buses, in bars, at parties, gets one an understanding of another society that can be gotten in no other way (even if Professor Wells' course helped lay the groundwork for all that!). In those extraordinary times, I knew more about the "disappeared" journalist Jacobo Timerman—why he was kidnapped and why his story, since well documented in print, was not the simple heroic saga presented in the American media—than the US State Department seemingly did. I got so into things Argentine that many years later, when Juan Peron's hands were severed from his corpse and held for ransom, I was the one who first decoded the ransom note, which was written in the argot of Hermetic mysticism—and I published the translation. My second homeland, indeed! In the old days, major newspapers had "stringers" in major world capitals, who were in a position to interpret events with the wisdom acquired over decades. I was a bit like that.

This reminiscence has been only tangentially about butterflies. It's about how my adult life evolved in a direction I could never have imagined back when I was undergraduate and how, looking backward, one can see how it all actually makes sense. I suppose that my life actually is about butterflies, but the living of it has involved some very unexpected turns. Contingency!

Two final anecdotes:

The Montoneros were a leftist guerrilla movement that grew out of the Peronist Youth. Peronism had a split personality, politically: the right, more-or-less-fascist wing followed Juan, while the left idolized Evita, who was masterful at co-opting the rhetoric and symbolism of class struggle. (One position, articulated by a Peronist theoretician named John William Cooke, held that Argentina was too primitive sociopolitically and economically to progress directly to socialism; it had to pass through a left-wing Peronist stage first.) The Montoneros were originally idealistic, but as so often happens, their movement devolved into senseless violence. It was largely the excesses of the Montoneros (assassinations, kidnappings, robberies to finance the movement) that were used to justify the coup that removed Peron's widow, Isabel, and brought the military to power. I knew a Montonera. Many of her colleagues in the movement were "disappeared" by the regime, but she somehow survived, and years later I encountered her—now thoroughly reformed, and working as a barmaid. I stayed and she closed up the place, and we lingered on much of the night talking about the past—and the future. She said "Communism failed. Russia failed; China failed; Vietnam failed; Cuba failed. *We must find a way to reinvent social justice from the bottom up.*" We're still looking.

One particular atrocity under the Pinochet regime so outraged me that I declared a personal boycott of Chile. I was an invited speaker at a scientific meeting there and had accepted the invitation, but now I retracted my acceptance in an open letter to the president of the conference. Knowing "*liberacion*" was seen as a Communist code word, I circumvented it by writing in my letter "I will return to my beloved Chile to celebrate its inevitable unchaining *(desencadenamiento)*." After Pinochet lost the plebiscite and retired, I was again invited as a plenary speaker. The meeting was held at a teachers' college. I went and introduced my talk by briefly recounting that story. And here I am, I said, to help celebrate your unchaining. And I got an overwhelming response from the audience. Afterwards, one of my hosts said "So someone told you the history of this place?" "No…." It turned out that the institution had been a hotbed of Allende socialism and had suffered horribly under the dictatorship, with faculty and students "disappeared" and tortured or murdered. I had indeed said exactly the right words at the right place.

Oh, yes, I did collect some pierids on that visit. I generally do.

Art Shapiro has been studying butterflies since age 10 or 11. Along the way, he got his PhD at Cornell in 1970. He is supposed to be a pierid specialist but keeps collecting undescribed skippers and Lycaenids in South America, which he passes on to real taxonomists to deal with. He has published about 300 papers and has turned out 17 PhDs, several of whom are brighter than he is. He enjoys Argentine and Uruguayan folk music and food and is a connoisseur of cheap beer. He has been at the University of California, Davis, since 1971 but spends about 250 days a year in the field in one hemisphere or the other.

Chapter 5
Pursued by Adrenalin, in Pursuit of Dopamine

Greg Ballmer

Tiger got to hunt, bird got to fly;
Man got to sit and wonder, "Why, why, why?"
Tiger got to sleep, bird got to land,
Man got to tell himself he understand.
the Prophet Bokonon in Kurt Vonnegut's *Cat's Cradle*

As water rose rapidly from the floorboard to seat cushion, my hopeful anticipation of a fine day collecting lycaenids quickly changed to desperate concern. The front of the vehicle was hung up on a submerged rock, while the spinning rear wheels dug deeper into the sandy river bed. Then came the sinking realization that water flooding into the rear of the vehicle was submerging luggage, including a week's worth of entomological collections and a couple US$1000 worth of film and photographic gear. Our little 4 WD Toyota Prado was stuck in the middle of the Xedon (Don River) in Saravane Province, southern Lao People's Democratic Republic (Lao PDR, aka Laos). Perhaps I was predisposed to find myself in this predicament (Fig. 5.1).

There may be a gene for fascination with Lepidoptera, as one of my earliest memories (perhaps dating to late toddler stage) is of crawling in pursuit of a lawn skipper *(Hylephila phyleus),* a flyswatter in hand. Some of my acquaintances with a similar mania for Lepidoptera can relate their own formative childhood experiences. And once old enough to know the term "entomology," I had a name for my passion, which eventually focused on Lycaenidae, and then further on lycaenid life histories and larval morphology. I settled on a field with seemingly endless possibilities for novel discoveries, which I have endeavored to record photographically (a companion passion).

Other deeply rooted factors leading to my career path (and Lao predicament) include fascination with neophilic sensory experiences (especially exotic sights, smells, and tastes), predisposition to "go farther," and willingness to accept the associated risks. There must be a hormonal component, as well, because the effort of exploration, accompanied by novel discovery, is frequently rewarded by elation.

G. Ballmer (✉)
University of California, 5894 Grand Av., Riverside, CA 92504, USA
e-mail: gballmer@gmail.com; ballmer@ucr.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_5

Fig. 5.1 John Burton's Toyota Prado SUV stalled in the Xedon, Saravane Province, Lao People's Democratic Republic (PDR)

Thus, in summer 1967, with a fresh bachelor of science (BS) degree (Entomology) in hand, I accepted an invitation to join a Peace Corps group (Thai XXI) destined to help eradicate malaria in Thailand, a land of which I knew very little. My job as a malaria entomologist lasted three memorable, life-altering years, including seven malaria infections. I was embedded in a culture where even mundane activities (e.g., striking a match, peeling a mango) had been independently invented and, though differing in technique from my cultural training, were at least equally effective; time and time again I was reminded that yes, indeed, there are more ways than one to skin the proverbial cat. Subsequently, Thailand has become a comfortable second home to be visited as often as possible. In addition to providing a satisfying feast for the senses, Southeast Asia is home to a high diversity of Lepidoptera, including many representatives of all lycaenid subfamilies, most of whose life histories are yet to be recorded.

The family Lycaenidae includes many species having close ecological associations with ants (Figs. 5.2 and 5.3). Such symbioses range from mutualism, in which lycaenid larvae provide attendant ants with nutritious secretions in return for protection from predators, to social parasitism in which the larvae prey on homopterous insects tended by ants and, in some cases, even dwell within ant colonies, where they solicit regurgitations from workers (trophallaxis) or feed on immature ants. Ants depend on an array of tactile and chemical cues to mediate their behavior, and lycaenids are just one of several insect groups (notably including some Coleoptera, Diptera, and Hymenoptera) to "crack" the ants' signal codes in order to exist within ant societies. Lycaenid larvae mediate their ant associations by means of substrate-borne vibrations and a variety of cuticular secretory organs. Tiny perforated cupola organs and specialized setae apparently secrete semiochemicals which mimic ant aggregation and/or nest-mate recognition pheromones or (in some cases) perhaps simply render the larvae unrecognizable as potential prey. Finger-like tentacle organs (TOs), usually adorned with branched setae, on the 8th abdominal segment of many species are normally withdrawn into the body, but can be extruded when larvae are prodded or attacked. Extruded TOs often elicit increased ant attendance and/or aggressive behavior among attendant ants, suggesting the release of semiochemicals which emulate ant alarm and/or aggregation pheromones. Many lycaenid species also have a dorsal nectary organ (DNO) on the 7th abdominal segment, which secretes a nutritious fluid attractive to many ants.

The variable presence and/or prominence of ant association organs and the composition of their chemical secretions may account for the diversity of ant associations among lycaenids. While some lycaenid larvae seldom or never form stable ant associations (Fig. 5.4), others may be attended by any of several ant species, and yet others are invariably associated with just one or a few related ant species. By the same token, ants which form stable associations with larvae of only a few lycaenids are often highly antagonistic toward other species. For example, members of the hairstreak genus *Flos* are invariably and exclusively attended by ants of the *Dolichoderus thoracicus* species group (Figs. 5.2 and 5.3), and *Spindasis* larvae are invariably associated with ants in the genus *Crematogaster*. Similarly, polyphagous

Fig. 5.2 *Flos fulgida* larvae construct folded leaf shelters, which they share with ants of the *Dolichoderus thoracicus* species group

Fig. 5.3 As with other *Flos* species, *F. apidanus* larvae share their folded leaf shelters with ants of the *Dolichoderus thoracicus* species group. The larvae emerge to feed nocturnally and even consume portions of their own shelters

Fig. 5.4 *Curetis saronis* larva displaying its exaggerated tentacle organs in response to potential parasitism by a tachinid fly

larvae of *Anthene emolus, Arhopala pseudocentaurus*, and *Hypolycaena erylus* are invariably associated with the arboreal weaver ant *(Oecophylla smaragdina)*, which excludes most other lycaenid larvae (and other ants) from its foraging territory (Figs. 5.5 and 5.6). For lycaenids having such highly specific, and perhaps obligate, ant associations, the suitability of a particular host plant or oviposition site depends on the presence of their respective ant associates.

It seems that there are always more questions than answers. One that continues to intrigue me concerns the genus *Curetis* (subfamily Curetinae), whose larvae seldom, if ever, form stable associations with ants. Nevertheless, *Curetis* larvae are notable for having highly developed TOs, which emanate from prominent cylindrical extensions of the body. Although larvae of *Curetis* often share their host plants with other lycaenid larvae, ants in attendance of the latter generally ignore the *Curetis* larvae. Even when those ants are in close proximity to *Curetis* larvae, their behavior appears to be unaffected when the latter are prodded to evert their TOs. Although extrusion of Curetis's TOs in response to prodding is consistent with a defensive function, modification of ant behavior is apparently not part of that function (Fig. 5.4). The quest for understanding goes on.

But I have digressed. What of the Lao PDR connection to my Xedon predicament? The Lao people are "kissing cousins" of the Thai and were included in the Thai kingdom until the late nineteenth century when French colonial expansion forced the Thai king to cede territory east of the Mekong River. Because landlocked Lao PDR is relatively poor, sparsely populated, and rural (also war-torn from 1942 to mid-1970s), economic development and entomological exploration have lagged behind its more populous neighbors (Burma, Cambodia, China, Thailand, and Vietnam). Lao village life is laid-back and reminiscent of rural Thailand of the late 1960s, before the latter became swamped by Western influences and economic growth. But all that is changing rapidly because the Lao government has embarked on an ambitious development program and promotion of tourism since the year 2000.

My fellow adventurer, John Burton, is a kindred spirit in entomophilia, wanderlust, and enthusiasm for Thai and Lao cultures. John had been my Peace Corps Vol-

Fig. 5.5 *Anthene emolus* larva attended by arboreal weaver ants (*Oecophylla smaragdina*). *A. emolus* larvae feed on a wide array of shrubs and trees colonized by *O. smaragdina*

Fig. 5.6 *Arhopala pseudo-centaurus* larva attended by weaver ants *(Oecophylla smaragdina)*. Weaver ants attend and aggressively protect larvae of a few lycaenids, while excluding other species from their foraging territories

unteer predecessor in the Entomology Division of the Thai National Malaria Eradication Project (Thai XI, 1965–1967), and, over the years, we have shared numerous adventures exploring those lands. John has a particular fondness for Laos, where he and his wife resided from 2001 to 2004. He refers to that period as the "sweet spot," when travel throughout the country was becoming possible, yet remote areas had not yet been overrun by tourists, and lumber companies had not yet cut down all the forests. John subsequently published *Lao Close Encounters* (Orchid Press, 2005), which pictorially records Laos the way it was. When John invited me to join him on an entomological excursion to southern Laos, it was an offer I could hardly refuse.

John's primary entomological interest is Tabanidae of Southeast Asia; his Cornell dissertation was published in 1978 as "Tabanini of Thailand North of the Isthmus of Kra." His secondary goal in Laos was to visit every one of its 141 administrative districts, some of which were still seasonally accessible only by motorbike, elephant, or on foot. No living person was likely to have set foot in all the districts, but John was nearing that goal and planned to knock off one more remote district after crossing the Xedon that fateful day in January 2003.

When traveling through rural Laos, contingency is a constant fact of life, and one should always expect the unexpected. We purchased gasoline as often as we could because fueling stations were scarce and often out of fuel. We carried as many different maps as we could find; all were inaccurate, but some were better at depicting roads, while others were better at provincial and district boundaries and still others indicated points of interest. When designated national highways turned out to be merely cow paths through rice fields, we asked directions from local villagers; but most villagers never traveled far from home and could only guess the distance and direction to the next large town. Unexploded ordnance was a constant concern, as much of eastern Laos was traversed by the notorious Ho Chi Minh Trail (actually a broad network of roads and trails), where American bombers destroyed as much infrastructure as possible during the "Secret War" of the 1960s and 1970s.

The road from the small provincial capital of Saravane (destroyed in the war and still in an embryonic stage of rebuilding in 2003) was rough, yet passable until we reached the Xedon. All that remained of the old French-built bridge was the blackened concrete supports. The water was clear, shallow, and placid at the near shore, where wheel tracks led down to the water's edge; but where they reappeared on the far shore (maybe 100 m away), the water was ominously a bit swifter and more turbulent. Lao rivers often fluctuate as much as 40 ft in depth between wet and dry seasons, but because January is the middle of the dry season, the Xedon was near its lowest ebb. Our initial caution, already weakened by anticipation of exploring new territory, was overcome when a local farmer assured us that vehicles regularly crossed where we observed wheel tracks. But those were mostly high-clearance trucks and rural buses. Our little sport-utility vehicle (SUV) only made it half way across the Xedon that day.

When forward progress ended, and reverse gear only caused the vehicle to sink deeper, John shifted to neutral and kept his foot on the accelerator (blowing exhaust bubbles out of the submerged tail pipe) until the carburetor sucked in enough water to kill the engine. A small group of water buffalo swam leisurely out to investigate our plight. After piling as much baggage as possible above the seats, I waded back to shore (camera and personal collecting gear held high) to seek help. Eventually a high-clearance logging truck arrived and pulled our vehicle back to shore and then all the way back to Saravane. We arrived late in the day at the one and only repair shop. The proprietor was away to repair a broken bus near the distant Vietnam border and was expected to be gone for a few days. No problem; we could leave the vehicle (as if we had a choice), and the teenage apprentice mechanics would tend to it in the morning. We transferred our bedraggled luggage and supplies via local taxi to a hotel, where we could unpack and assess the damage.

A clothesline (packed in my baggage for just such a contingency) was strung around the hotel room and soon draped with wet clothing. Fortunately, my precious insect specimens and film had been safely stored in water-tight food containers and plastic freezer bags. But photo gear did not fare so well. Although my camera was unscathed, water had penetrated to the inner elements of one of my two macro lenses, and my electronic ring flash was wet. Gently shaking the lens allowed most of the water to drain out, but residual moisture condensed on the inner elements, rendering it unusable. And the first subsequent use of the ring flash was accompanied by a loud “pop” and a puff of smoke; so much for that item.

A determined photographer, faced with equipment failure, must rely on ingenuity, and I was determined to carry on. After all, a lot of new territory and potential new entomological prizes remained to be photographed before this adventure (optimistically) might end. It occurred to me that a sheet of aluminum foil could be fashioned to create a reflective hood for my remaining (non-ring) flash unit, when attached to the flash shoe atop the camera, to deflect the normally forward-directed light path downward to illuminate a subject just in front of my remaining macro lens. A trip to the local open-air market for aluminum foil was fruitless. It was difficult to describe what I wanted, as no merchant had ever heard of such an item. Aluminum foil is normally used for covering items to be baked in an oven or stored in the refrigerator, neither of which applied to the local residents. However, I found large plastic pouches of imported hard candy, bright pink on the outside but with a highly reflective aluminized inner coating. That turned out to be even better than aluminum foil for my purpose when carefully cut, folded, and taped into the proper shape. My jerry-rigged substitute for a ring flash proved adequate, and, as a bonus, I had a supply of tasty candy. The show could go on.

The next day, back at the repair shop, we watched the kids drain the fuel tank into a large metal basin, remove the water contamination, dismantle and clean the carburetor, blow out the fuel line, dry the electrical components, and then reassemble it all. Meanwhile, three cows wandered by and began drinking the strange urine-colored fluid in the basin. An alert mechanic shooed them away and poured the remaining petrol back into the fuel tank. After some anxious moments, John tested the ignition; the engine sprang to life, and we drove away with considerable relief and elevated spirits. We celebrated with a side trip to a local waterfall tourist site. Later, John would have his vehicle thoroughly inspected by his mechanic in Vientiane, but for now our adventure could continue. There would be more entomological riddles to ponder, more precarious situations to escape, and ever more sensory delights.

From Saravane, John and I spent another week traveling further southeast to the crest of the Annamite Range on the Vietnam border, before returning to Vientiane with priceless memories and entomological specimens. We crossed more streams, visited remote hill tribes, and traveled for a while with an unexploded ordnance (UXO) disposal team, but there were no more dramatic incidents to compare with our attempted Xedon crossing until…. Another week later, on our way to visit Ra Island in South Thailand, John and I found ourselves adrift in a dingy with a dead outboard motor (and without a paddle, of course) on a moonless night in the shipping lane of Khuraburi Bay. But that is another story.

> There are known knowns. These are things we know that we know. There are known unknowns. That is to say, there are things that we know we don’t know. But there are also unknown unknowns. There are things we don’t know we don’t know.—Donald Rumsfeld

Greg Ballmer spent his early years chasing butterflies and raising caterpillars in the Bay Area, Salinas Valley, Bakersfield, and Riverside, California, as his family gradually migrated southward. He received his Bachelor of Science (BS, 1967) and Master of Science (MS, 1973) degrees in ntomology at the University of California, Riverside, with an intervening stint in the Peace Corps

(1967–1970), attached to the Entomology Division of the Thailand National Malaria Eradication Project. Those were formative years in embracing new cultural paradigms and becoming enamored of Thai food, photography, and foreign travel. The next 30+ years were devoted to researching integrated pest management methods for cotton, lettuce, strawberries, grapes, and citrus (to pay the bills). All the while, he has continued to study life histories and larval morphology of butterflies (especially Lycaenidae), with annual return visits to Thailand, his adopted “home away from home.”

Chapter 6
Mount Shasta and the Mystery of Mu

Felix Sperling

I had a window seat on a commercial flight over northern California when I first saw Mount Shasta's intriguing cone. Of course, I immediately thought that it would be cool to collect butterflies on this large dormant volcano. I am a lepidopterist, after all.

A month later I was at Mount Shasta. My wife Janet, an entomologist herself, had let me talk her into combining a family camping foray with a research trip to collect tortricid moths. I was a newly appointed assistant professor at UC Berkeley, and my colleague Jerry Powell had recommended a couple of sites in the area for spruce budworm moths. My field notes say that we arrived at McBride Springs National Forest campground, on the southwestern slopes of Mount Shasta, shortly after 5 p.m. on August 8, 1996. I write field notes so that I don't forget the important stuff. It also keeps things real. That's needed at Mount Shasta.

But now we were all hot and tired. It was a 5-h drive through the blazing Central Valley, the only air-conditioning in our tiny Nissan Sentra being an open window. Our two boys, aged 5 and 7, had reached their limit. They were packed in the backseat like sardines, camping gear stuffed all around them. And my dear, ever-supportive Janet was 6 months pregnant. This was as far as we were going to go today. End of discussion.

Fortunately, we arrived to an empty campground, with level sites and a bit of shade.

Oddly empty.

We were expecting motorhomes. But it was a Thursday, and Janet pointed out that it was also the first time I had actually left work early enough in the day to beat the traffic. So, we drove around the campground circle, paused at the entrance a second time to make sure that there were no restrictions, and picked a nice site. Soon the groundsheet was down and we were in the midst of trying to assemble our brand new REI dome tent.

F. Sperling (✉)
Strickland Museum of Entomology, Department of Biological Sciences,
University of Alberta, Edmonton, AB T6G 2E9, Canada
e-mail: felix.sperling@ualberta.ca

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_6

Within minutes, another car started slowly around the campground circle. I silently congratulated myself on our early arrival, which let us get a good spot. But the car stopped at our campsite; two lean and leathery men in an otherwise empty vehicle. One stuck his head out and shouted, “You hear about the mountain lions?”

“What?” I was confused. I must have heard him wrong.

“Yeah, there was a mountain lion right here yesterday. And they’re going after dogs down in the valley. Careful with your kids. You better leave.”

“Gee, thanks for letting us know!” That was all I could think of saying as I walked toward the car to find out more. But the driver stepped hard on the gas, and they were gone.

Oh damn! Better pack everything up and look for another campground, far down the road. No sense in risking my family with a hungry mountain lion. One had recently taken down a jogger in central California. I knew the danger was real.

And yet, something was not right. Why did those Good Samaritans leave so abruptly? Why was nothing posted at the campground entrance? Why did they creep along the road so slowly as they came into the campground? But maybe I was rationalizing because I was tired and just didn’t want to pack everything up again. From a basic cost-benefit analysis, it was simple. Just get out.

Janet and I talked about it. We reasoned that we would be wedged between trailers soon anyway, with beer-fueled discussions, throbbing generators, and bright lights across the campground. Why leave? And until the other campers arrived, we would do what we always did on our walks in the Berkeley Hills, surrounded by heavy fog as the little ones pretended they were in Tolkien’s Mirkwood. Just keep the kids close to us and stay alert. We did the same on Berkeley and Oakland streets, where there was a sizeable population of homeless people, many of them undeniably mentally ill. And I have to admit that I get stubborn and defiant when I’m feeling pushed around, whether by people or predators. We decided to stay.

Then the boys started to squabble, as kids do. They needed to burn off some energy. So, we had to explore our surroundings, which I always do anyway at new campsites. Janet stayed with the car. Off we went, down an interesting path through the scrub, me sternly reminding the boys to carry a stick and to stay close. Would you have done that? Maybe not. But I doubt you grew up as I did, roaming freely through forest and swampland. I want the same freedom for my children.

The boys and I took our time exploring the incense cedar and white fir, getting several hundred yards down a dry trail and into long needle pines. Suddenly, I noticed something far out in front. I told the boys to get behind me, as calmly as I could, and tried to listen. I saw it again, a large tan-colored shadow among the trees, coming quietly and quickly toward us. It would be futile to run back up the path with two little kids; all the official descriptions of wildlife encounters say that just invites an attack. Heart thumping, I started to whistle and tried to consider whether a mountain lion could be most effectively disabled by jamming the wire rim of the net down its throat or by poking the end of the handle into its eye. Hmmm—I needed a backup plan. I picked up a fist-sized rock.

“Daddy,” my 5-year old whispered behind me. I ignored him.

Again, more insistently, “Daddy.”

I shushed him. This was certainly no time for discussion. There was a large dangerous animal bearing down on us.

But he wouldn't shush. Next came his loudest whisper, "Daddy, she's not wearing any clothes."

In a moment, I saw it was true. A tall suntanned woman with long blonde hair emerged from the trees, wearing nothing but sandals. I quit whistling, feeling foolish. She strode toward us with the fluid motion of someone who spent her life covering ground. I dropped my rock behind me, hoping she didn't see it, and shifted my grip on my net to look less threatening. She kept coming. I forced myself to politely look up at her head, not her chest. Her age was hard to guess, maybe 40. A few more steps and she reached us. I mumbled hello, and moved aside. She nodded and carried on with no discernable change in pace or facial expression. A few steps and she was around the corner and gone. My oldest son giggled.

Janet had a good chuckle when the boys and I got back. Naked hippies were not such a big deal. Back home, the boys had already watched more than one official How-Berkeley-Can-You-Be Parade, with its bizarre selection of nudists, nuts, and ninjas. Besides, this one was too sensibly shod to be crazy. And surely a calm, lone, local hippy indicated that mountain lions were not a concern. We wondered where she was heading, as she certainly wasn't staying at our campground.

It was just as well that we were feeling calmer about cougars that evening. Not a single other camper came to use the campground. I still think that's odd, considering how well populated every other campground was on our trip. Nonetheless, I put the thought aside and focused on the main reason we came to Mount Shasta. I put up two black lights on opposite sides of our campsite and checked them regularly until midnight. My family told me that they slept soundly, including when I crept quietly into the tent, bringing a big hunting knife with me. I barely slept.

In the morning, we asked the campground garbage pickup crew about mountain lions. They said there had been no incidents or sightings anywhere near there.

That day we drove further up the road to the mountain, climbing up an avalanche chute to about 9000 ft elevation. Numerous *Hemileuca* moths sailed past and I caught one for my PhD student Dan Rubinoff's thesis project while I scouted out better sites to place a black light. We convinced ourselves that the guys who warned us about mountain lions were just trying to discourage us from staying because there was a camp with nudists in the back country. It was not apparent where they parked their cars, though.

That evening, Janet and the boys stayed back at the campground, which finally had a few people occupying other sites. I drove our car up a road that angled up the southern slope of the mountain, stopping at Everitt Vista Point. It had a long parking lot where I set up my black light and sheet at a panoramic spot. I caught a number of tortricid moths that evening, some in old-style cyanide bottles and others in clear vials on ice for DNA extraction back at the lab. But the evening had another memorable surprise for me.

It started in the gathering darkness, with my black light already up and the white bedsheet behind it reflecting its light into the night. First, a car drove in and parked on the far end of the lot, then several more until there was a tight cluster. About a dozen people emerged in unison, conferred for a few minutes and started walking straight toward me. Big people walking fast, some of them carrying sticks and others carrying lights. They marched purposefully toward me as a group, while I silently rehearsed what I would say when they got to me.

"Hi, I'm just collecting moths for a research project. Yes, I do preserve a few of them, but they don't suffer. Really."

No, that was too defensive.

Or perhaps just "Hello, how are you?"

That seemed too calculatedly oblivious.

But by now they were almost upon me. I gripped my butterfly net firmly. Twice in 2 days.

Then 20 ft from me, without a word, the whole group turned sharply and plunged off the edge of the pavement onto a dark trail. It was a narrow, difficult path, and I heard the clattering of rocks and shoes for many minutes, ever more distantly. This was strange. They seemed fully clothed. But it was hard to be sure in the dark.

Suddenly, I heard a long, desperate cry. The sound echoed far up a gulley, and then the darkness was rent again a bit closer to me. Frantically, I tried to decide what to do. Should I take down my black light immediately? Or should I leave it there and drive as fast as I could to the nearest town? But I didn't know whether to report a mountain lion attack or a brutal ritual murder.

I know it sounds crazy. But I've been chased off a ranch in Colorado, shotgun pellets plinking all around me as the rancher tried to "get my attention." He later said he was taking no chances after finding that the previous trespassers on his land, just a few days before us, had ritually slaughtered a group of his cattle. But I digress.

This evening, those spine-tingling, drawn-out cries became two, then four, then a whole choir of voices echoing down the mountain. In a moment, eeriness transformed into ethereal. Breathtakingly beautiful singing filled the pitch black night for the next hour, with clear tones carried on the fresh mountain air, a memory that I'll carry for the rest of my life. And a mystery.

I tried to turn to the moths attracted to the ghostly sheet behind my black light, but I was too enthralled and mesmerized by the concert. Then, the night fell silent. Several minutes of rattling rocks marked the group as they returned, the first ones emerging suddenly beside me. Not one of them stopped or even turned their head as they silently passed my black light. They all seemed to have much weightier things on their minds, striding one by one to their cars and immediately driving off.

I did collect a few moths. They ended up being used in five different PhD theses: two in Berkeley and three in Alberta. Their DNA sequences have been deposited in GenBank many different times. In their own way, these fine nocturnal insects have become immortal. And their collection data are indelibly associated in my mind with a symphony of soulful sound that begged for an explanation.

We got back to Berkeley a few days later, still pondering our experiences at Mount Shasta. Just a bunch of hippies—that was the consensus from all the people I asked. So, I kept asking. Eventually, I told my story to Doug Kain, who had just finished a PhD project in my lab on the population genetics of Lyme-vectoring ticks. He had a wealth of experience that ranged from being a Vietnam war veteran to working in Stan Prusiner's lab where prions were first discovered, and he had lived in Humbolt County long enough to appreciate the phenomenon of Mount Shasta.

Doug only laughed: "You just visited a portal to the Kingdom of Mu."

I had no clue. I looked at him grinning, assumed he was talking about sacred cows, and said: "Oh really? Like moooooooo?"

"Oh no—like Atlantis. Mount Shasta has a gateway to a continent called Mu, spelled M U. It's really Atlantis and there are special caves there that let people in."

And here I thought Atlantis was off somewhere under the Atlantic. Now it was in California. I didn't believe him. But it was true. Just google "Kingdom of Mu" and you'll see it for yourself.

I'm a little unclear on the details, and there are contradictory stories out there on the World Wild Web. But it seems that there are secret Atlantean gardens under Mount Shasta that are tended by an advanced society of human beings[1]. Some say they are 7 ft tall, and some say that they are small and only partially visible because they live in three and a half dimensions[2]. They occasionally come out among us to dispense their immortal wisdom. Apparently they mostly wear white robes, but I'll bet that sometimes they don't wear anything, just like the long-limbed lady we encountered at the McBride Springs campground. Or maybe her clothes were in another dimension. Fascinating stuff.

If you want to know more, you'll be happy to learn that the mysteries of Mount Shasta and Mu have been monetized. It started with a prospector called J. C. Brown who found a cave full of gold and crystals and other good stuff, although the town full of eager believers that he recruited were not so happy when he disappeared. Now you can donate (credit cards only, please) to a global organization called Telos that gives tours to the portals to Mu[3]. You can also buy guided meditations from the same group, at $25 for a set of two CDs[4]. The part I'm most curious about is the "beloved little booklet" in which Angelo the cat speaks to the people of the planet. I wonder if Angelo is a mountain lion.

Anyway, it seems that in 1894 Fredrick Spencer Oliver published a book that described how survivors from a sunken continent called Lemuria are living in tunnels under Mount Shasta. Surely, they sing beautifully too, and if you are really lucky, you can catch their concerts at the Everitt Vista Point. Of course, this is not a static culture. For example, the name Lemuria is now often shortened to Mu. Very elegant and simple, as befits a sophisticated race, don't you think?

The name Lemuria, it turns out, can be traced to the biogeographer and ornithologist Philip Lutley Sclater, a contemporary of Darwin, who in 1864 hypothesized a land bridge connection between Madagascar and India, explaining why lemurs are found on both land masses[5]. His delimitations of zoogeographic regions continue to be used with little change, but his concept of Lemuria has been taken over by

1 http://atlanteangardens.blogspot.ca/2014/04/secret-city-under-mount-shasta.html.

2 http://www.lemurianconnection.com/category/about-mt-shasta/.

3 http://www.lemurianconnection.com/category/about-mt-shasta/.

4 http://www.mslpublishing.com.

5 http://en.wikipedia.org/wiki/Lemuria_(continent).

a delightfully eclectic array of other social forces. These range from writers about the occult to Tamil nationalists, who associate Lemuria with ancient greatness now sunken somewhere beneath the Indian Ocean, the Pacific Ocean, or Mount Shasta. All I can say is that this makes for great tangents in my class lectures on biogeography. I wonder if Sclater would be shocked or amused if he were to come back to life to see how his concept of Lemuria has evolved and speciated.

Since I am on the subject of the transmogrification of words, I would be remiss if I didn't point out that this cultural process occurs so rapidly that my experience at Mount Shasta already falls into a different time stratum. I recently told my story to a group of students and used "cougar" instead of "mountain lion" to describe the large predatory creature that I was worried about before encountering a nude woman. They burst out laughing, then had to explain to me that a cougar is an older woman dating a younger man. So were the two guys in the car just playing a joke on me about a human "cougar"? Not likely. Our encounter happened 3 years before the first recorded use, in 1999, of "cougar" in its new social connotation[6].

Life as a lepidopterist is full of these kinds of rich and crazy experiences. A brief sighting of an intriguing mountain turns so easily into a trip down rabbit holes of the human imagination, past and present, where I can combine the personal with the professional and still get paid. And almost 20 years later, I can proudly say that my family and I are still exploring piquant paths, predators be damned (Figs. 6.1 and 6.2).

Fig. 6.1 Our two sons, Bill and Ed, on the upper slopes of Mt. Shasta, August 9, 1996, where they helped me chase after *Hemileuca*. It did not occur to us to look for lost civilizations in caves

[6] http://www.thestar.com.my/story/?file=%2f2007%2f10%2f17%2flifefocus%2f19059904&sec=li32 fefocus

Fig. 6.2 Me demonstrating lepidopterological focus at a black light sheet on my Berkeley balcony a couple of years after our Mt. Shasta foray. Bill stands guard with a net, while our third son, Andy, is wondering why mom is laughing as she takes the picture

References

Barrett G (2007) Time for a cougar? The Star Online. http://www.thestar.com.my/story/?file=%2f2007%2f10%2f17%2flifefocus%2f19059904&sec=lifefocus. Accessed 3 Nov 2014

Mount Shasta Light Publishing. http://www.mslpublishing.com. Accessed 12 Nov 2014

Secret City Under Mount Shasta. http://atlanteangardens.blogspot.ca/2014/04/secret-city-under-mount-shasta.html. Accessed 12 Nov 2014

The Lemurian Connection. http://www.lemurianconnection.com/category/about-mt-shasta/. Accessed 12 Nov 2014

Wikipedia: Lemuria (continent). http://en.wikipedia.org/wiki/Lemuria_(continent). Accessed 12 Nov 2014

Prof. Felix Sperling has been fascinated by Lepidoptera ever since he found a Glover's silk moth on his way to school in 1966. His focus soon shifted to trying to determine how many species were represented by the swallowtail butterflies at his parents' farm at Bragg Creek, Alberta. His interests have since expanded to understanding species' boundaries, population genetic processes, and phylogenies in a variety of arthropods, but particularly North American butterflies and moths. He received BSc and MSc degrees (with George Ball) from the University of Alberta, and a PhD from Cornell University (with Paul Feeny), and was a postdoc at the University of Ottawa. He was a professor with the University of California at Berkeley before taking advantage of the opportunity to return home to Alberta as a professor in 1999. Of the more than 50 students and postdocs that Felix has mentored over two decades, most of them have stable teaching and research positions at universities and museums around the world.

Chapter 7
How and When I Ventured into the Study of Butterflies and Adventures Along the Way

Lawrence E. Gilbert

At some point in my adult life, I began to reflect on how I came to allocate so much time to observing butterflies and on many adventures I had along the way. Like many children growing up outside of poverty and with opportunity to experience nature, I found fascination in all things, especially living things. By the age of 12, my bedroom was a small museum covering geology, archaeology, and natural history. Twelve years later, butterflies had become a major focal point as I contemplated graduate school. After another 12 years, I had already associated with a number of contributors to this volume, either as student, advisor, or colleague. We were all being paid to teach, conduct research, and interpret nature's patterns from a strong lepidopteron perspective. We all seem to have reached this point with very diverse personal histories and personalities. Thus, I am as curious about my colleagues' experiences as revealed in this volume as I am about recalling and assessing my own personal turning points that brought me to be counted in this strange assemblage.

Because of some odd twists of family history, I grew up being exposed to biogeographically diverse and interesting environments. My paternal grandfather died in the flu pandemic in 1918, and papa (Lawrence Sr.) and his baby brother were raised in a Masonic children's home in Florida for their formative years. My grandmother fished them out after 10 years and soon dropped them in San Antonio on her way to California to live near her friends. Thus, papa was left to take care of his younger sibling while unsuccessfully trying to finish high school. After working in Dallas for a few years, papa was allowed to enter Austin College in Sherman, TX, on probation. His goal to be a Presbyterian minister helped this Presbyterian college decide in his favor.

Meanwhile, my mother's family was "Old Texas" all the way. Mama's mitochondrial linage arriving with the second Austin Colony in 1827, into the Mexican state of "Coahuila y Tejas" and many other of her ancestral branches moved in during days of the Republic or just after the Civil War. Her father, Ira Burns, had,

L. E. Gilbert (✉)
Department of Integrative Biology, University of Texas, Austin, TX 78712, USA
e-mail: lgilbert@austin.utexas.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_7

with his dad, surveyed the family ranch just south of the Nueces River: 2000 acres that was acquired in 1906, during the last episode of homesteading in the lower 48 states. As a teenager, Ira stayed on the ranch to fulfill homestead provisions so that his sibling could go to school. Thus, his formal education ended in the eighth grade. My mama, Mildred, was proud of being valedictorian of her senior class in Catarina. However, there were only three graduating students and the other two were cowboys. My granddaddy sent her to Austin College so she would not marry one of these local boys. There she met my dad. Papa was about as alien to South Texas as one could be. Much later, we learned he was the grandson of a Union Officer (from Gilbertsville, New York) who had escaped from the Confederate prison in Andersonville. Papa had no extended family to visit on holiday, so my mother's clan adopted him.

The important thing for me as a young naturalist was that wherever mama and papa lived, we would travel to her family's anchor point at Catarina near the Mexican border for thanksgiving, Christmas, and summer breaks. I was continually exposed to changing biotas as we lived in various ecoregions (Fig. 7.1), and from

Fig. 7.1 The combined larval colors and odors of black swallowtail, *Papilio polyxenes*, combined to make my encounter with this species in 1953, near Jones Creek, Texas, my first distinct memory of a butterfly

there would travel to Catarina, by then a near ghost town. It is situated in a vast semiarid Savannah grassland known as the "brush country." In my youth, the region was largely as the Spanish had described it in 1684, when they passed through searching for the French colony led by the explorer LaSalle. Instead of isolated trees scattered through grassland, this Savannah was composed of shrub clumps in the grassy matrix. Each clump can be composed of a variety of woody shrubs, vines, and cacti, and as many as 12 woody plant genera might co-occur in such clumps, many being adult or larva host plants for butterflies such as cloudless sulfur, snout butterfly, hackberry butterfly, and lyside *(Kricogonia)*. Almost everything has thorns and my favorite was a plant called "all thorn" *(Koeberlinia)* which has nothing but green stems and thorns. Horned lizards were common. I also grew up thinking this was the homeland of collared peccary until I saw them in Costa Rican rain forests later!

Papa not only served as a regular minister, he was also a Navy Chaplain and a Chaplain for the Texas Department of Corrections in between serving small town congregations. He truly believed and lived what he was preaching and that did not set well with some of his "free-world" flocks when it came to "all men equal in the eyes of God." Opposition to non-Caucasian races being included in these churches was accompanied by a sincere belief by some that "Negroes and Mexicans have a separate Heaven"! Looking back, I can see why we moved frequently from town to town in West Texas, to North Central, and finally around the central Gulf Coast south of Houston. I attended ten different schools before college, including one on Midway Island during the Korean War. Everywhere we lived, whether the manse of a local church, an island navy base, or Texas prison farm, I found myself on the edge of great expanses of pastures, oceans, woodlands, and agricultural fields. Periodically, I would be transported with the family back to the South Texas mesquite rangeland where granddaddy Burns had become a major honey producer with 1100 hives scattered across several vast ranches including the former family ranch lost in the depression. In my teenage years (late 1950-early 1960s), I spent summers helping with the bee business. Everywhere nature was interesting and available. Best of all, I had parents who found nature interesting and who considered study of God's creation a noble way to spend time. I was not compelled to have a summer job.

It seems that while all children are explorers on a newly colonized planet, the lucky few like most authors of these chapters were able to explore nature under the tolerant and protective eye of sympathetic adults. For me, such favorable social and natural environments reinforced a broad interest in natural history. Oddly, emergence of my interest in butterflies had to do with saying goodbye to an island paradise in 1952. While I do recall fish, birds, horned lizard, rattlesnakes, honeybees, *Polistes*, deer, sea urchins, snails, and jackrabbits prior to that date, I do not recall any awareness of butterflies. In October 1951, my mother took us three kids to join papa who was already deployed at the naval base on Midway Islands. Thus, at age 9, I had the run of a mid-Pacific coral atoll for most of each day. Such atolls sit on the peaks of seamounts, and this one was on the remains of one of the earliest volcanoes in the Hawaiian archipelago. Midway was teeming with seabirds like

Laysan and Black Albatross, tropic bird, fairy tern, brown boobie, shearwater, and frigate birds that rely on such scattered patches of coral sand to exploit remote parts of the Pacific Ocean. The coral reef drew my interest but I could only imagine what was out there from what washed in on the beach over night. Midway school ran only 4 h a day for a given grade level. In our magical 13 months on Midway, I developed an intense interest in marine invertebrates, especially Mollusca of genera *Cypraea* and *Conus*, both with fabulous diversity on the atoll. I was struck by the elaborate patterns of cone shells and by the fact that periostricum covered the pattern of live ones I saw and by the warning that some species were deadly if handled.

After our return to the mainland in 1952, papa became pastor of an historic church at Peach Point in Jones Creek, Texas. It had been built on part of a plantation owed by —"Father of Texas"—Stephen Austin's sister. The minister's residence next to the church sat adjacent to a large prairie bounded by hardwood forests along the Brazos, San Bernard, and Colorado Rivers. Ironically, some of the best remaining old-growth hardwood forests remaining in North America are here at the western edge, a3-h drive from the arid brush lands along the Mexican border (Fig. 7.1). There we were situated in the top winter birding area of North America. I recall seeing snow geese and long-billed curlew out behind the house. Inspired by a book my parents gave me, by John James Audubon, I subscribed to the Northwestern School of Taxidermy's course by mail and sat about making study skins of the birds I shot with my .410 shotgun. For a time, I retained an interest in marine life and greatly anticipated our family's initial trips to the beaches between Freeport and Galveston. I was quite keen to continue the study of marine mollusks. Unfortunately, I was greatly discouraged by the chocolate brown surf colored by discharge of nearby sediment-laden rivers and by oil slicks, tar balls, and trash that fouled the beaches. This coast was a far cry from a pristine atoll with white coral sand, turquoise water, and colorful organisms. Sadly, the beaches of tiny remote Midway are now fouled with tons of plastic garbage.

One day while exploring the pasture near our house at Peach Point, I found a gaudy caterpillar with an unforgettable odor and eating wild umbellifer. I brought plant and larva to my mother. She suggested that I put the plant in a pop bottle between my bedroom window and its screen so I could watch what happened. After a few weeks I was watching a black swallowtail, *Papilio polyxenes* emerge (Fig. 7.2). I became transfixed by conversion of plant to butterfly via caterpillar and obsessed with attempting to capture tiger swallowtails on the woodland edges. I retain vivid memory of several people stopping their car on the lane near our house, in about 1954, all running into the pasture with butterfly nets in pursuit of large butterflies I could only watch in frustration.

I have always wondered who those collectors were. Texas was not home to many lepidopterists in those days. The two that come to mind as collecting in early 1950s were H. A. Freeman, skipper specialist, and Roy O. Kendall, who described host plants and life histories for many butterflies in southern Texas and northern Mexico. No doubt a specimen label in some museum collection with a 1954 date and Jones Creek, Brazoria County, TX, location, would reveal the name of one of the persons trespassing in the pasture near our house. A good guess for an

Fig. 7.2 *Left panels* show the "brush country" of South Texas east of Catarina. *Right panels* show the old-growth river bottom hardwood forests south of Houston where my family lived during the 1950s. In a3-h drive to visit grandparents, I was exposed to dramatically different ecoregions

out-of-state visitor might be Harry K. Clench on an expedition from the Carnegie Museum in Pittsburg. After reading some of his papers as an undergraduate at UT Austin, I wrote Harry asking to go with him on a tropical expedition and after the Mexico trip I describe below, I sent him specimens I could not identify. One was a species new to science.

On visits to South Texas family, I had noticed pupae suspended by silk girdles on the stucco walls of my grandparents' church in Catarina. These turned into *Battus philenor,* pipe vine swallowtail, that seemed quite fantastic (Fig. 7.3). This was during the famous 1950s drought. Later, I understood that pipe vine swallowtails are able to persist in dry times because host plants have storage roots and can continue staying green. In retrospect too, I know that the pale yellow lyside and snout butterflies hanging around the Burns' home during winter were adults in diapause. Both species respond to post-drought rains by undergoing mass migrations. I vividly recall these spectacular events as the drought ended in the mid-1950s. Cars and trucks would overheat from all the butterfly bodies covering radiator grills (Fig. 7.4)!

In 1956, papa became chaplain in the Texas prison system, and we moved to the 18,000-acre maximum security Ramsey prison farm along the Brazos river bottom, south of Houston. We rode the school bus to Angleton, 18 miles from the headquarters (HQ). At the time, extensive old-growth hardwood bottomlands were being cleared by hand to keep prisoners occupied. Large fields were cultivated

Fig. 7.3 *Battus philenor* was the first life history I worked out as a kid, starting with pupae on walls of my grandmother's church in Catarina. I spent hours following females searching for host *Aristolochia longiflora*, the leaves of which were grass-like and hard to pick out

by thousands of inmates with guards patrolling on horseback. By that time I had constructed an effective butterfly net, and had the run of pastures, fields, Oyster Creek, and the edges of ponds for fishing and bug collecting. The cultivated alfalfa fields were boiling with alfalfa butterflies, but I also took notice of gulf fritillary and skippers with long tails. It took a while to learn that packs of bloodhounds bearing down on a person would treat one like a stump as long as one's odor was not the training odor. On visits south to Catarina, I was now trying to find *Battus* host plants in by following females. I recall my first views of great purple hairstreak visiting extra-floral nectaries of black-eyed peas in granddaddy's garden and magically coming out of nowhere to drink water droplets when the Catarina yard was watered during dry hot summers.

Before we left Ramsey for Sugarland's Central I Prison farm in 1957, I donated a cigar box of crudely pinned butterflies to my middle school science class in Angleton. Central Prison is now gone and Sugarland's Imperial Sugar refinery closed. The town welcomed Fidel Castro on a visit in 1959, before his intentions were clear. The area was long ago overrun by Houston's southwesterly expansion. But in the late 1950s, it was quite rural. Unlike the isolation of Ramsey, dirt roads across Central Prison farms property were accessible to those wishing to traverse the area from HW 59. I was now in high school and participating in major

Fig. 7.4 Snout butterfly, *Libytheana bachmanni* undergoes massive population outbreaks and migration when rains break extended drought in South Texas. Butterflies clog car radiators and dead bodies litter roads. This phenomenon was one of the things about butterflies that I found most interesting as a youth

team sports, and a few of my football teammates might have been mistaken for rednecks. Certainly my strange habit of running around collecting natural objects was a source of amusement and teasing at school. One day a pickup load of guys, apparently, up to no good, intercepted me walking alone with a butterfly net. When they demanded to know what in the heck I was doing, my response of "catching fish bait" was an honorable enough explanation to send them on the way without needless altercation.

To this point, my butterfly interests were totally without the support of outside information. Aside from my Audubon book and Heyerdahl's *Kon-Tiki* (a book grandparents had given me with all the bad words carefully marked out in blue pen), our house was devoid of books on natural history or science. A watershed for me came when papa enrolled in a Psychological Counseling Masters Degree program at the University of Houston (U of H). The first thing I remember from that was him pulling me aside after his course on human sexuality and telling me to forget everything he had taught about the evils of masturbation. Better yet, he used his library access at U of H to check out books that allowed me to identify specimens in my Hawaiian shell collection and, most importantly, Holland's *The Butterfly Book*. The latter allowed me to take my butterfly interest to another level. I was fascinated by the general idea of specific host plants as a key to finding and rearing butterflies since I was beginning to figure it out for myself. Soon I was seeking more current books on my own. I was excited to find Klots *Butterflies of Eastern North America* in a bookstore and bought a copy.

After that our homeland in South Texas became even more interesting since many butterflies listed by Klots in the North American fauna "occasionally strayed

Fig. 7.5 My first encounter with a zebra longwing, *Heliconius charithonia,* in San Antonio, Texas, 60 years ago may have influenced my research career

northward" from the neotropics. Thus, I began to urge that family trips include places further south (Brownsville, Pharr, McAllen, etc.) where such rarities had been collected. I clearly recall the shock of seeing my first *Heliconius* (Fig. 7.5). It was a zebra longwing in the Sunken Garden of San Antonio's Brackenridge Park. Papa saw me easing over to collect it off a *Lantana* flower and quickly told me that collecting this insect in a public place was not appropriate. I can only wonder if this denial fueled my later foray into *Heliconius* biology.

Our family continued to be on the move within the same area south of Houston. Papa left prison work in summer 1960, and returned to "free world" ministry near West Columbia where we lived my last year of high school. I enrolled as biology major at UT Austin in fall 1961, having left specific interests in organismal groups behind, at least temporarily. I continued to be interested in butterflies, but there was little time to pursue such study with no car and no obvious associated career path. Besides, intercollegiate athletics and heavy course loads left little spare time. My interest in butterflies and host plants did lead me to sign up for classes in entomology and botany. In 1963, Papa bought a 17-acre tract of land from Phillips Petroleum that at the time was part of unbroken forest along the San Bernard River. That summer I helped him build a cabin on the site and encountered my first *Lethe portlandica*, a large satyr butterfly known as pearly eye existing there on the south-western extreme of its range. A bamboo *(Arundinaria)*-feeding butterfly like *Lethe* flying in a palm understory only a few hours level drive from the semiarid cactus and mesquite rangelands around Catarina fueled my interest in biogeography.

Also in 1963, I stumbled across Ivan Sanderson's *The Continent We Live On*. His chapter on the Mexican Sierras seemed to explain where tropical butterflies straying into South Texas might likely originate. Tropical semievergreen and evergreen forests lay only a few hours south of Brownsville, TX, on the eastern slopes of the Sierra Madre Oriental, just south of Victoria Tamaulipas. Having no car, I talked my roommate Hardy Morgan (now a retired physician living on his Ranch near Hico, TX) into driving mycology Grad student Fred Kiefer and me south in June 1964. My intent was to see the northern extent of the tropics. We got as far as El Salto Falls in San Luis Potosi where we saw *Morpho, Hamadryas, Biblis, Heliconius, Eueides, Dryadula, Anartia, Anaea,* and *Eunica,* etc. It was a full cast of neotropical seasonal forest species that continue from there to Panama and beyond. Ironically it was soon after, collecting for entomology class over Christmas break of 1964, that I recorded the first US record for *Dione moneta* (Fig. 7.6). My younger brother and helper, Tom, netted it near the house in Catarina. I, later, learned that this heliconiine was typically found in mid-elevation neotropical wet forests. My first publication described the conditions associated with its appearance in Texas.

Thus, intrigued by the abrupt end to most neotropical butterflies just south of Texas, I was excited to see a graduate seminar listed in the Geography Department organized by a Professor Donald Brand entitled *The Temperate-Tropical Transition in NE Mexico and Southern Texas.* I jumped in immediately and found myself in company with several zoology graduate students, including the late herpetologist, evolutionary biologist Craig Nelson. Craig had been my T.A. in Ecology a semester before and was important now in helping me chart my next path. I had chosen to write my term paper on the biogeography of butterflies across the region, but I had little to go on except a synthesis by William Hovanitz that placed the steepest part of tropical butterfly diversity decline at 20° N latitude in Veracruz.

The first of two critical things Craig Nelson did for me was to point out Paul Martin's 1958, University of Michigan dissertation monograph on *The Biogeography*

Fig. 7.6 *Dione moneta* ovipositing on *Passiflora adenopoda* in Hesperia, Ecuador, in 2008. *D. moneta* uses the same host in the mountain of Tamaulipas, Mexico. Finding this butterfly in South Texas during Christmas 1964 further stimulated my interest in the distribution of tropical butterfly faunas

of Reptiles and Amphibians in the Gomez Farias Region, Tamaulipas, Mexico. Martin's mapping of vegetation zones and listing of floral elements in this isolated patch of semievergreen tropical forest provided the key to predicting the butterfly fauna, yet to be properly explored in the 1960s, and that became my paper topic. Later, this effort formed the basis for my undergraduate NSF research proposal that funded my solo expedition to the region in summer of 1965. The second thing Craig did for me was to inform me about the Organization for Tropical Studies Fundamentals of tropical biology course in Costa Rica and I began to plan for that for the following year. Organization for Tropical Studies (OTS) courses were just getting under way in the mid-1960s, and would come to be seen as the basic training ground for tropical biology and portal for many students wanting to work in the Neotropics. I was very fortunate to learn about this opportunity when I did.

Meanwhile, in the 1964–1965 academic year, I was in the Botany Department's honors program. That involved sitting with each faculty member for a week or two doing selected readings. On my own I had already found Lincoln and Jane Brower's 1964 Birds, *Butterflies and Plants: A Study in Ecological Chemistry* and C.T. Brues's 1928, American Naturalist paper Coordinate Evolution of Butterflies and Plants. Butterflies were beginning to seem more viable for a research focus. When it came time to study with phytochemist Ralph Alston, he immediately directed me to a new paper in the journal *Evolution* by Paul Ehrlich and Peter Raven on butterfly plant coevolution. I was already drifting this way but this paper helped seal the deal. Moreover, I noted that the Browers had written their synthesis paper while at Oxford with E. B. Ford, so when Fulbright Fellowships were announced the next year I applied. Likewise the Stanford group seemed like a good place to pursue butterfly research in an ecological and evolutionary framework.

Preparing for the Mexico trip in spring 1965, I spent many hours in the UT Herbarium learning to recognize plants that characterize the vegetation zones described by Martin. Through UT botanist Marshall Johnston, I met Fred and Marie Webster, Austin-based birders who knew the Gomez Farias area and knew Frank Harrison, the man who had hosted Paul Martin at his cloud forest finca "Rancho El Cielo." I borrowed wooden expedition boxes from the UT Geography Department supply room, and left via Catarina and Laredo in my hand-me-down 1961 ford station wagon loaded with supplies for collecting butterflies, plants, lizards, snakes, amphibians, and myxomycetes for various UT collections and professors.

Arriving in Gomez Farias, I left my car behind the thatched house of Senior Vargos, Alcalde of the municipio, loaded my supply boxes on a burro led by a slight fellow named Nicholas Morales who had agreed to guide me to Frank's clearing 8 miles and 2500 ft above Gomez Farias. The walk-up on June 24 took 5 difficult hours. It was hot, and humid, plus I had been very sick and bedridden the week before. I lived with Frank and took many 1–2-day hikes into different habitat types accessible on his side of the mountain. Parts of the cloud forest grew over a vast number of limestone spires, sticking up like the statues of Easter Island. Orchids, bromeliads, and ferns covered these formations. I once became totally lost by going off-trail in that area. Luckily, Frank's dog had gone with me and showed me the way home. On one walk to ridges above and west of Rancho Cielo, I was caught by darkness and heavy rain and luckily found an old shed at what Frank said was a former barium mine. My host expressed his extreme angst over my not returning when expected and mentioned having to haul students out of a sinkhole.

At the time, I did not know that Harrison had more to worry about than the hernia he won for his heroics saving students. On one hike, I took a wrong turn and stumbled into the clearing of squatters. They were clearly sullen and hostile so I backed out quickly. Later, I learned they had an ongoing feud with Harrison and recognized his dog. Their dogs attacked Frank's dog and me, yet these men took no helpful action. I have never before or since stared into such cold dead eyes. I carried Frank's .22 pistol in my knapsack at his urging but these fellows did not know that. After that I had the habit of stepping off trail and standing still when hearing people coming ahead. Big cats do the same I later learned. Just 6 months later these men would hack Frank Harrison to death one Sunday morning, and send their wives over an hour later to steal his belongings.

On the 1965 field trip, I hoped to sample butterflies in all the diverse vegetation zones described by Paul Martin. So, when a group of high school boys climbed the mountain to visit Frank from the village of Adolfo Lopez Mateos, home of the Chamal colony, a farming and ranching community on the southern end of Martin's vegetation map of the area, Frank said that it would be worth my while to follow them home. The Taylor boys' grandfathers were prerevolution Anglo-American settlers who went to Mexico on land grants on an agreement that they would teach Mexican campesinos new farming methods and help them become independent. When the revolution started, the men buried belongings, sent women and children to Texas, and hid out in the mountains. This way as peace came, they could quickly reoccupy houses and farms. I learned that Frank Harrison was a Canadian who in the 1930s had been a schoolteacher in the Chamal colony. He and other men from the colony had explored the mountains to the north of their village, and had come across a cloud forest containing temperate-zone trees like beech and maple from the north and *Podocarpus* from the south. It seemed an ideal climate for a Canadian and for his gardens of vegetables, flowers, and fruit trees. When the girl Frank had hoped to marry chose another man in the village, Frank headed for where I found him 30 years later.

To get to the town of Adolfo Lopes Mateos (formally Chamal), I had to walk down to Gomez Farias, drive east in a road = landing strip through cotton fields being aerially sprayed with DDT. I then proceeded south to Cuidad Mante. I bought supplies there and drove west on the road towards Ocampo. Unfortunately, the bridge over Rio Comadante had been washed out and traffic was crossing a pontoon bridge that terminated on the other side at a steep muddy bank. I saw that it was either maintain good momentum and make it up the bank with my two-wheel drive ford or go too slow, not reach the top, and slide sideways into a raging muddy river. That was a close call with disaster! Once past that hurdle I took my time and collected butterflies along the road. Surrounded by pastures and patches of dry tropical deciduous and thorn forest, the butterflies I collected there were much as one would find as occasional rarities in South Texas. I rolled in to the village of Lopes Mateos, and met the Taylor boys at the town plaza where local kids hung out, drank refrescos, and played music on a jukebox. That was my first time to hear the Beatles sing “Yesterday.” That music, relief of surviving the river crossing, and viewing the south end of the mysterious Sierra Madre Oriental backbone as a mist blue-green backdrop, created a pleasant moment always remembered.

Over the next 2 weeks, I was kindly hosted by various families of the Taylor clan. Seymour Taylor provided the best opportunity. His father had been an original settler in the valley and settled a ranch that sat in the afternoon shadow of an extinct volcano called “Chamalito.” He put me in the now empty house of his father, and I experienced my first kerosene refrigerator. From that base, I set fruit traps for nymphaline butterflies like *Anaea*, and spent a hot day thrashing through thorny plants to reach the sharp peak of Chamalito. My local guides were the same boys I met at Frank’s rancho. In the 1990s, I saw these boys in Austin at a Chamal colony reunion. These then middle-aged men remembered that day and were surprised to meet up again with the “butterfly guy.” Chamalito’s peak was a magnet for male butterflies from the surrounding landscape using it as a place to attempt rendezvous with virgin females (Fig. 7.7). A spectacular red and black male of *Siderone nemesis* was captured there chasing about with a swarm of males of diverse species including large *Atlides* hairstreaks. From the Taylor ranch HQ, I also followed a trail 6 miles to reach the southern edge of the tropical evergreen forest (called Paradise Valley) that Martin’s maps indicated to be a well-isolated patch separated by a belt of dry forest. This southern edge of evergreen forest was determined by how the Sierra Madre intercepted moist coastal winds. Once the backbone of ridges swept lower and westward, rainfall on the slopes and lowlands to the south was not adequate to support moist forest. Butterflies certainly informed me that I had entered evergreen conditions. Blue morpho, the tiger-patterned *Heliconius ismenius,* the spectacular *Prepona laertes* (Fig. 7.8), and many other indicators of the Neotropical realm were what I had come to see!

While based on the Taylor ranch, I drove around the lowlands collecting the edges of the evergreen forest wherever I could access it by road. I noted things like blue *Morpho* showed up whenever I entered that formation. I drove back to collect more intensively around Gomaz Farias. On July 21, I encountered a robust, sweaty, and red-faced man on his hands and knees just off the trail below the town. I had encountered Professor Bill Brown. Bill was a famous myrmecologist from Cornell University busy collecting ants. I stayed the night with Bill and his group of Cornell students, among them an undergraduate named Bob Silberglied interested in butterflies. The Cornell group provided great entertainment in Gomez Farias. Each night a crowd of men, women, and children gathered around their black light for attracting insects and laughed with delight when a gringo reacted to being bitten or stung. Without doubt, Bob would be writing a chapter for this volume had he been fortunate to live a full life. Sadly, he perished in Air Florida’s crash into the Potomac in January 1982.

I returned to Rancho Cielo from Chamal on July 26. This time I beat Morales and his burro to Frank’s by a full 2 miles. By then I was in great shape from running about after butterflies in these rugged mountains. The goal was to sample in the dry side of the range and the settlement of La Joya de Salas was the start point. I knew some of the caving club guys from my classes at UT, and they had tried to set a world depth record in repelling down the estimated 5000+ ft depth of the sinkhole

Fig. 7.7 The peak of Chamalito was boiling with hill-topping male butterflies of numerous species. One of the Taylor boys used my camera to document my presence there in July 1965

Fig. 7.8 Just as I was about to swing a 12 ft net at this male *Prepona laertes,* he exploded off his perch to chase another butterfly. His iridescent *blue* flashed in the bright sun over the canopy in the valley below Gomez Farias. I was watching with binoculars when at about 400 m out he turned and headed back. On a guess, I held my net at his original perch and was able to catch him. This species is a striking indication of evergreen neotropical forest where the host tree *Inga* is present

that dominated the center of the La Joya basin. They had packed 13 burro loads of rope up from Juamave in the desert to the northwest (NW) and below, and spent 10 grueling days in the hole before giving up 1900 ft down. I was taking sufficient risks on the surface to venture into a place with no butterflies and leaving the first rope without a guard! So I already knew about this area, but getting there from Frank's rancho was a very long walk.

Luckily, the same day Dr. Barbara Warburton from Southmost College, Brownsville, visited us and planned a drive over range to La Joya de Salas where she had contacts who might assist me in exploring the high chaparral vegetation in that sector. Warburton along with trustees of the college was then building a field station on Frank's land and some of them had built personal cabins there. So on the 29th, I travelled with Warburton and was introduced to the six siblings of the Osario family. Their parents were not present.

I stayed in the boys' hut and food was served in the third thatched building. It took me a few hours to realize that pigs eliminated the need for outhouses (privies) and sewer system. The oldest boy, Juan Osario, guided me to low Chaparral at 7000 ft and 8 miles NW of the village. For several days, we camped in the most desolate spot I have ever experienced. At night, I could hear the church bells in the town of Juamave in the desert below. We ate a rabbit I killed with a slingshot, and some sorghum tortillas. Butterflies were abundant but the most striking was the cycad-feeding *Eumaeus deborah.* Juan and I were starving when we staggered back into La Joya de Salas. The scrambled eggs and black beans his sisters fixed for us remain my most memorable meal in seven decades!

In early August, I made a quick run to the border for shoes. (UT grants accountants would not recognize this as a travel expense!) I did not want to waste time so I turned around and went directly back, arriving at Gomez Farias at dusk. I was an hour up the logging road with heavy pack and weak-yellow headlamp. It was misting and my view of the trail was fuzzy. I did not bother to avoid a stick in the trail, and instantly felt something hit my boot. I stepped on and turned the light behind to see a gorgeous snake. Since I was also collecting herps, my first tendency was to grab it. However, the triangular head of *Bothrops atrox* (Fer-de-lance) came into focus and the folly of messing with deadly pit viper in that situation made me hesitate and leave it alone. In that moment, I learned that I needed glasses! Later I learned about this snake in Costa Rica. I realized that had the strike been an inch higher, my boy scout "cut & suck" snakebite kit actually would have reduced my chances of survival to nil as it was 9 p.m. with no hope of help until morning. This serpent injects venom as nasty as its colors are beautiful: anticoagulants, hemolytic, and protein-digesting enzymes as well as neurotoxins. Luckily, I lived on to find other ways to almost perish while working on butterflies!

Combining my Mexico experiences and the emerging literature on butterfly plants interaction, mimicry, and ecological genetics, a life of researching butterflies seemed appealing, feasible, and rewarding. But any plan to continue studying in the eastern sierras of Mexico was dashed with the murder of Frank Harrison. But I had fallen in love with tropical forests and sought them out further south. Sadly, drug cartels now make the Gomez Farias region even more dangerous for field research than it was 50 years ago.

After graduating from UT Austin in 1966, I took another brief plant and butterfly expedition to the summit of Cerro Potosi, Nuevo Leon, Mexico, using written instructions from botanist John Beaman who had done the floristics of the mountain. I was then off to the OTS fundamentals of tropical biology course in Costa Rica where I discovered the Osa Peninsula and encountered an Assistant Professor from University of Kansas, Dan Janzen. Dan's main influence on many of us was to inspire confidence in approaching biology from a strong base of natural history. The OTS experience helped me better interpret the things I had seen in Mexico as a naive observer and reinforced my butterfly bias. When our course travelled to Panama and most of the class explored trails on the Barro Colorado Island, I chose to park myself in the BCI library to page through for the first time some of the rare and only books then available on neotropical butterflies. Great field biologists such as Phil DeVries would later fill the void of butterfly field guides for the region.

Returning to Texas in late August, I had only a few days to pack for my Fulbright year with Professor E. B. Ford at Oxford. In Great Britain, Ford was best known for his two fine books on moths and butterflies, but abroad he was known for pioneering population genetic studies on butterflies and moths that combined demography and genetics. His book *Ecological Genetics* had attracted my attention; I moved into an office just vacated by his DPhil student, John Turner. John kindly toured me through his work on races of *Heliconius* at the British Museum of Natural History in London. I helped Ford with fieldwork on *Maniola jurtina* and encountered a cast of characters ranging from Bernard Kettlewell and Philip Sheppard to Miriam Rothschild. Briefly engaged with eyespot variation in *Maniola*, I sent a reprint request to Boris Schwanwitsch in the U.S.S.R. for reprints of his papers on the nymphaline ground plan. His widow replied and sent her husband's book and reprints with a bleak and melancholy photo of his tombstone in Leningrad, the latter engraved with his idealized butterfly wing (Fig. 7.9). Ford's later graduate student, Paul

Fig. 7.9 Nymphaline ground plan on the tombstone of Boris Schwanwitcsh in Leningrad. Sent to me with a set of reprints by his widow

Brakefield, soon occupied the office I vacated next to Professor Ford and, finally, a proper study of eyespots ensued.

One memorable experience was driving E. B. Ford and Theodosius Dobzhansky (Fig. 7.10) to Ford's famous study site at Cothill, Berkshire, where he and R. A. Fisher had conducted his classic studies on demography and genetics of the day flying tiger moth, *Panaxia dominula*. Ford had nominated Dobzhansky as foreign member of the Royal Society and his induction was reason for the visit. Dobzhansky was a Russian ex-patriot famous for work on chromosome variation in natural populations of fruit flies and the integration of genetics into the modern synthesis of evolution. Ford was very proud to show "Dear Doby" around, although he received constant teasing from his friend as we drove. "Henry" Ford as friends called him did not regard women, other than Miriam Rothschild, to be the equal to men intellectually or otherwise. Dobzhansky teased him that they were equal since one X chromosome was silent (the Barr body). I was not sure why Ford introduced Professor Dobzhansky as "the world's greatest horseman" to the bar tender at the pub where we stopped for lunch, but clearly it was part of their good-natured but edgy bantering. *Panaxia* images in Fig. 7.10 were the

Fig. 7.10 E. B. Ford and T. H. Dobzhansky collecting *Panaxia dominula* at Cothill, Berkshire, in 1967. Such day-flying moths must be accorded status as honorary butterflies!

ones I collected or reared from larvae found on that trip. I am pleased to have an excuse to publish my images of this unique encounter of two great evolutionary biologists in the field.

I went on a field trip to the Isles of Scilly with Kennedy McWhirter, a barrister and friend of Ford who dabbled with butterflies. Kennedy's twin brothers were the originators of the "Guinness Book of World Records" as well as being famous Scottish sprint champions. He seemed to be in their shadow and shared Ford's distain for the Labor Party and humans bearing two X chromosomes. When a driver in our way was not performing well, it was probably "a filthy woman." As we drove southward, I heard many stories and strong opinions about global politics, WWII, and field work with "Henry." I recall Kennedy always smelling vaguely of alcohol and vomit. This was all very new for this rural Texas kid. Driving south we sampled meadow brown butterflies, *Maniola jurtina*, from Ford's various study populations in southern England. Kennedy would calculate chi-squares in his head as we sampled and would break off work to head for the nearest pub when significance was reached. I am not a great statistician but I was somehow suspicious of this approach!

Arriving in Penzance, we took the Scillonian to the Isles of Scilly. This ferry routinely specialized in transporting tourists across shallow seas and had no keel. All was sunny and fine until a brief squall hit the ship. Decks were quickly awash in vomit from hundreds sitting in park benches on deck. Below must have been hell. I survived a brief bout of nausea by moving to the stern and watching seagulls diving for the remains of many breakfast, now being poured overboard by the cleanup crew. The birds seemed to know what was coming as they had been following us ever since we sailed hours before!

The sun was shinning as we pulled into the harbor on the main island of St. Mary's. Harbored in the bay was the shimmering white Royal Yacht: Someone said Queen Elizabeth was there for a celebration of sorts. The next morning I stood shirtless holding a net bag of live butterflies in the open window of my first floor hotel room on St. Mary's when the entire royal family drove by in the narrow cobblestone alley no more than 10 feet away! Prince Phillip was at the wheel of the long-bed land rover convertible. The Queen was to his left and royal kids were in back. Just past my window and up the hill was a 6 feet high rock wall on which children were sitting in wait for the entourage. The land rover was not going to make the turn on the angle Prince Philip was driving. He became flustered and stalled the vehicle. He then shifted into neutral and rolled back down the hill for another try. This time when they drove up the hill, I had my shirt on!

Much of my time in Oxford was spent in the Hope collections and library and its great holdings of specimens and literature specialized on butterfly mimicry assembled by E. B. Poulton and Hale Carpenter. Audrey Smith, Hope librarian, was pleased to have me visiting and gave me a few things to return to Professor Ford. She said that when George Varley was appointed Hope Professor to replace Hale Carpenter, Ford never returned to the collections. Audrey also gave me many reprints from the old days, a copy of the collected "Hope Reports" and the last distribution copy of a privately assembled volume "Mimicry" assembled by Poulton for his friends: The classic three papers on mimicry by Bates (1862), Wallace (1865), and Trimen (1869)! Ironically former Oxford undergraduate, James Mallet, would later make good use of these resources in Texas when he was a PhD student in Austin.

One day Audrey Smith informed me that a finishing Oxford undergraduate was also talking about going to work with Paul Ehrlich at Stanford University. She had suggested he talk to me. A few days later someone with horned rimmed glasses and bushy red hair knocked on my door. It was Mike Singer, wanting to know if Stanford had a good academic reputation. He had applied there based solely on a publication on *Euphydryas editha* by Paul Ehrlich's graduate student, Pat Labine, but he had not heard of Stanford otherwise. With only slight trepidation, Mike was prepared to head "across the pond" and into the unknown to study *Euphydryas*. After almost half a century, Mike's focus on checkerspot butterflies has not diminished, although the red hair dropped off decades ago (Fig. 7.11)!

In August 1967, I married a girl from Midland, Texas, who had been in third grade with a cute (but not so brilliant) kid named George Bush. Christine Mast must have guessed what she was in for because after we met in 1964, I was off to Mexico or Costa Rica every summer. Our honeymoon trip consisted of a road trip through Mexico collecting butterflies when possible. I walked her up the mountain to Rancho Cielo only to find that the place was being guarded by a "pistolero" because Frank's killers were already released from the prison in nearby Xicotencatl. They were back on the mountain since no one else could care for their families! The caretaker, Lucas, was Frank's helper when I was there before. He kindly shared what little food he had. We had arrived without notice.

Our honeymoon trip continued to Mexico City and then up the West Coast where I was amazed to see large white morpho butterflies crossing the highway in low dry forest. On a narrow curvy mountain road, I drove over a triangular rock that rotated under the car, knocked the motor off its mount, and weakened the rear suspension on our station wagon. Driving north of Hermosillo on a lonely highway soon after

Fig. 7.11 Michael C. Singer conducting host preference trials with *Euphydryas editha* in a rooftop greenhouse at the University of Texas, Austin, over 40 years after initiating work on these butterflies

dusk, I felt the car shutter and swerve. As I slowed down, all hell broke loose as the rear right suspension dropped from the frame and plowed into the road. This forced the wheel back against its well and caused the car to careen all over the highway before plowing a furrow in the verge and coming to rest. I was thus stuck in a desolate spot with all my personal possessions and my new wife. Christine surely must have been wondering how she went wrong in choosing a mate! Through the night she slept while I stayed awake and alert. I turned away several offers of help after midnight from carloads of men by gruffly saying *Todo esta Bien*. I certainly did not want to reveal our vulnerability or the presence of a woman in the car.

When the sun came up, I developed a plan to cut barbed wire from the nearby fence, jack up the broken suspension and wire it into place. There were several problems with the plan. First, I needed to pull the rear half shaft forward and needed a jack that could fit under the suspension. I had just looked in my dictionary to find that small hydraulic jack was "gato hidralico" and was planning to flag down someone to ask for one when a crew working on power lines came upon our pathetic situation. The foreman took one look and was clearly entertained by the challenge. He said he had to drop off the crew and would return. Thirty minutes later he was back. He had all the perfect tools, a "come-along" to pull the rear half shaft and wheel into place and a gato hidralico to raise the suspension back into place. We wired and chained it there according to my plan, but with the jack removed the suspension's leading edge hovered only 3 in. above the road's surface. We could not drive fast and risk bouncing!

About 10 a.m. with sun beating down, Christine started driving at a cautious 20 mph to Nogales, Arizona, while I slept. We arrived in late afternoon, and luckily found a welding shop that fixed the suspension for $15. According to the mechanic who first looked at the problem, this situation was not seen often because generally it was not survivable! The next day we were off to California and 2 days later we rolled by almond orchards that would become Silicon Valley and on into Palo Alto and Stanford. We were welcomed there by Mike and Pat Singer who were already settled in. Mike and I were office mates in Paul Ehrlich's lab for the next 4 years. For me, the smell of *Eucalyptus* still recalls the dry early September on the Stanford campus when we arrived in 1967, and my wonderful sojourn in grad school studying butterflies. Paul Ehrlich was just 35 years old then and already off on his human population crusade! Paul has not diminished that effort, and the problem becomes worse by the hour.

Before my dissertation work got underway at Stanford, I did OTS post-course research in early 1968. I went first to Les Holdridge's "Finca La Selva" just as he was selling the property to OTS. At that time, it was accessible only by boat from Puerto Jimenez and uncut forest covered much of the Costa Rica's Atlantic lowlands. I learned that climbing spikes were not useful for studying canopy butterflies. I then went to the Wilson's "Finca Las Cruces" near San Vito on the southern Pacific slopes of the Talamancas and found one of the richest butterfly faunas I have seen anywhere. Before OTS could acquire the Wilson property, many hectares of the forest I experienced in 1968 were to become cornfields. Sadly, a wonderful spot where I discovered males of two species of the pierid genus *Archonias* holding territories was destroyed before my next visit as a course resource person in 1972. I was leading a group using my own map drawn in 1968. The students laughed when I got lost following my own map. We had entered a cornfield not there to be mapped on my prior visit. To my dismay, the area was greatly degraded. On that trip I met Tom Emmel, who preceded me in the Ehrlich lab at Stanford, and Woody Benson, whose fine ecological studies of *Marpesia* and *Heliconius* remain classics.

Christine and I drove from California to Texas in January, 1969, and I expanded collecting sites in Mexico south to Valles, San Luis Potosi. I returned to Costa Rica to participate in the summer 1969, OTS advanced population biology course and studied ithomiine butterfly communities as my course research project. After that my attention swung to dissertation work. I travelled around looking for checkerspot butterfly populations beyond Stanford's Jasper Ridge where Mike was focused on studying larval biology. Meanwhile Paul had raised Ford Foundation funds for tropical work and we started studies in William Beebe's New York Zoological Station at Simla, in the Arima valley, Trinidad. This is where biological studies of *Heliconius* had started in the 1950s, and where my life with *Heliconius* butterflies began as well, thanks largely to Paul's grant.

My full conversion to butterfly biology happened in just 12 years between 1954 and 1966, was reinforced by fieldwork in 1967–1969, and by exposure to Mike Singer and Paul Ehrlich at Stanford. That chapter ended almost 50 years ago! During and after graduate school and into my academic research career, many twists and turns and interesting people, adventures, and near-death experiences have come my way in the course of studying butterflies, in encouraging others in that direction and in feeding off the influence of like minds with different perspectives. We authors have all been fortunate to live during these times on planet Earth and not to have outgrown a shared professional fascination with butterflies and moths.

Lawrence E. Gilbert Jr. is a professor of integrative biology at the University of Texas (UT), Austin, where he has taught and researched since finishing PhD work with Paul Ehrlich in 1971. He was the chair of the Department of Zoology at UT from 1990 to 1999. He has directed UT's Brackenridge Field Laboratory in Austin since 1980, and established an invasive species research program there. In the mid-1980s, he developed the first biological station at Sirena in Corcovado National Park Costa Rica. Although modest, this facility has provided a base for many unique rain forest studies by an international cast of graduate students. Larry has had the pleasure of learning from the diverse talents and knowledge of 43 PhD students who flowed through his lab as advisees or co-advisees. Half of these studied butterflies in some fashion, but the remainder addressed behavioral, ecological, and evolutionary questions by studying wasp, ants, hemipterans, primates, plants, frogs, birds, corals, and parasitoid flies. He encourages graduate student advisees to work from a strong framework of natural history and to develop their own strong identities and leadership roles in biology and conservation. Larry has participated as a resource person for many organizations for tropical studies courses in Costa Rica between 1972 and 2008. In addition to continuing work on the biology of *Heliconius butterflies,* their resource plants, *Passiflora* and *Psiguria,* and interactions of parasitic phorid flies and invasive ants, Gilbert has recently initiated studies on social behavior of male white-tail deer.

Part III
Discovery

Due to the efforts of Bill Nye, the Mars rovers contain the inscription, "To those who visit here, we wish a safe journey and the joy of discovery." Lepidopterists do not need to visit Mars to see this inscription because the message exudes from the workplace: it is the feeling you get when you open the museum cabinet, it creeps out of the code you write for statistical analyses, you can read it on the host plants of the caterpillars you collect, and it is written on the wings of butterflies that you search for throughout your career. The full joys of discovery and epiphany are almost always difficult to communicate on a written page, but many of the chapters in this book demonstrate such joy. The authors in Part III describe very different types of discoveries from their successful careers, all of which are exciting: the epiphany of metapopulations—an important theoretical approach for ecology; discoveries of many new life histories of tropical moths; and a lifetime of uncovering large-scale processes and patterns in insect–plant interactions.

Pterourus neyi neyi. Illustration by Brianne Boan

Chapter 8
One Butterfly Turned Me to Biology, Another One Helped Establish Metapopulation Ecology

Ilkka Hanski

In the 1950s and the 1960s, when I was a boy, it was common in Finland for children to spend school holidays at the countryside, in one's grandparents' place. I was no exception. My father had left his small village on the coast of the Gulf of Finland following the war, to settle down, with my mother, in the town of Tampere some 300 km away. Starting from the age of 4 months and until I had completed high school, I spent all my summers in my father's home village, in my grandmother's little house, with my brother and, during their vacations, with my parents. I and my brother had plenty of company, there were a dozen other boys and girls with comparable family histories, and local children as well. We had a wonderful childhood, complete freedom, to play whatever we pleased, to swim and to fish, and to spend all our time out of doors. In around 1961, one older boy started to collect butterflies and moths, and a few others followed suit, me included. We made our own butterfly nets and boxes for specimens, we stalked hawk moths in lilac flowers during the light summer nights, we searched for big caterpillars to rear big moths. For the others this lasted for two summers, but I never stopped. I suppose I was not a super social kid, I was happy to wander around on my own.

The Butterfly That Made a Difference

I cannot claim that I would remember many particular events related to butterflies from those early summers, but there is one exception. On August 18, 1964, when I was 11 years old, I walked 2 km from our village with my younger brother to an area with dry meadows, and I captured a butterfly that I could not find in my small book on insects. The specimen was preserved nonetheless along with dozens of others. In the autumn, my mother bought a bigger volume that included all the butterflies in Finland and other Fennoscandian countries (Langer 1961). It was not difficult to

I. Hanski (✉)
Helsinki, Finland
e-mail: ilkka.hanski@helsinki.fi

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_8

find the unknown butterfly—it was a female of the dusky meadow brown, *Hyponephele lycaon* (Fig. 8.1). What surprised and delighted me was that, according to my new book, this was an extremely rare species, not recorded in Finland since the 1930s. My father thought that I should let others know about it, and so I attended my first meeting of the local entomological club. From there, things started to roll on. My father, who had accompanied me to the meeting, had to return back home and fetch the very specimen for others to see. I was seriously questioned whether I was certain that this specimen had not been caught abroad.

The news about my butterfly was communicated to Professor Esko Suomalainen in the University of Helsinki, a population geneticist and a renowned lepidopterist, best remembered for his work on chromosome evolution in Lepidoptera. More important for my case, Suomalainen had published a paper on the extinction of *H. lycaon* from Finland (Suomalainen 1958). The species used to be quite widely distributed in southern Finland in the late nineteenth and early twentieth century, after which its range started to shrink and the last population went extinct around 1936. The decline coincided with a cooling climate after a short warm period in the 1930s, but Suomalainen was particularly interested in what happened in the last remaining populations. In his paper, he analysed phenotypic diversity as a proxy of genetic diversity—no means of measuring the latter, deoxyribonucleic acid (DNA) had just been discovered. He concluded that "the sudden final disappearance of the species from Finland is probably the outcome of the small size and isolation of these populations, which leads to the formation of homozygous and consequently uniform strains. The result is loss of capacity for adaptation with the possibility of rapid destruction if conditions change. Additional support for this hypothesis is afforded by the fact that the Finnish *Epinephele lycaon* specimens vary very little morphologically, whereas outside the frontiers of Finland, as close as in the Leningrad region, the variability of the species is considerable" (translation by Wolfgang Reschka from the original German text). Here is a remarkable early statement of

Fig. 8.1 The female of the dusky meadow brown *(Hyponephele lycaon)* that I collected on August 18, 1964, in Virolahti, southern Finland. Apart from the missing antennas and my fingerprint on the forewing, I did a good job in spreading the butterfly at the age of 11 years. I caught the butterfly from the very southeastern corner of Finland, close to the Russian border. Most likely the butterfly was a vagrant from Russia

concern about genetic deterioration in small isolated populations, a concern which properly emerged in population biology only in the 1970s.

By coincidence, research by myself and my associates on the Glanville fritillary butterfly, about which I have much to say below, has produced conclusive evidence for inbreeding in small populations increasing their risk of extinction. I believe that Professor Suomalainen would have been pleased to know about our results. But this happened much later, in the 1990s. Back in 1964, he had sent me a reprint of his publication on *H. lycaon,* which I could not read as it was written in German, but the reader of this essay can imagine the effect on an 11-year-old boy of receiving such a document. Collecting that butterfly, and receiving that reprint, made it practically certain that I would become a biologist. While in high school, I thought that I was destined to become a taxonomist in the natural history museum in Helsinki, but after entering the university I realized that I could as well become an ecologist, which was an enormously exciting field in the early 1970s, with several new subdisciplines being established, including theoretical ecology, behavioural ecology and conservation biology.

I have to confess that my enthusiasm for butterflies waned to almost nothing during my years as a student, first in Helsinki since 1972, where I did my master's thesis on blowflies, then in Oxford since 1976, where I did my DPhil, the Oxford version of PhD, on dung beetle community ecology. I became a population ecologist, and I worked on various groups of insects and small mammals. I became interested in theory and models, particularly models about the spatial distribution of populations in their habitat, and how this would influence their dynamics. The theory of island biogeography by Robert MacArthur and Edward O. Wilson (MacArthur and Wilson 1967) had a lasting impact on me. In the late 1980s, I started to work on what is now called metapopulation biology, absorbing the concept from the papers of another great American population biologist, Richard Levins (Levins 1969, 1970), who was my hero for a long time. Metapopulations are networks of local populations inhabiting networks of habitat patches. Local populations in individual habitat patches may have a substantial risk of extinction, but these are compensated for by dispersing females establishing new populations in the currently unoccupied patches. Thus, the metapopulation may survive even if all its component local populations have a high risk of extinction. Exactly what are the conditions for long-term persistence in real landscapes is not an easy question, however. I started to think about models to figure out the answers (Hanski 1983, 1989). Soon realizing my limits in mathematical analysis, I began collaborating with the mathematician Mats Gyllenberg, with whom I published several papers (Gyllenberg and Hanski 1992; Hanski and Gyllenberg 1993). But being an ecologist myself, I could not be content with theoretical results only; I wanted to start a research project to test model predictions. And here I returned, after 19 years, back to butterflies.

The Butterfly That Became an Icon of Metapopulation Biology

In the spring of 1991, my wife Eeva gave me a birthday present, a new award-winning volume on Finnish butterflies (Marttila et al. 1990). I had told her about my aspiration to start a new project, possibly on butterflies, and she wrote on the first page, "best wishes on your journey back to butterflies" (original in Finnish). I had been thinking of other taxa as well, including shrews, which to me are honorary insects, but I suppose my teenage enthusiasm for Lepidoptera started to creep back—and of course it would help that I knew butterflies well, I had spent 10 years chasing after them. There was also another factor. Professor Paul Ehrlich, one of the authors of the present volume, visited Helsinki in the fall of 1990, and I had an opportunity to talk with him about Edith's Checkerspot *(Euphydryas editha)* at Jasper Ridge near Stanford. I knew, of course, about his work (Ehrlich 1965), but it makes a difference to meet the person and to hear a first-hand account of the research. This is relevant here because when I leafed through the volume on Finnish butterflies in the early spring of 1991 to select a species for my research, to test model predictions about metapopulation dynamics, surely my discussions with Paul were back in my mind. I went through the entire fauna of 114 butterfly species (which is now 121 species, largely due to climate change) and thought about the pros and cons of every species, but at the end the choice was clear, the Glanville fritillary (*Melitaea cinxia;* Fig. 8.2), a close relative of the Edith's Checkerspot. I had never seen the Glanville fritillary alive, but I made up my mind based on what I read about its biology and occurrence in Finland.

The Glanville fritillary, like the Edith's Checkerspot and many other temperate butterflies, is a host plant specialist, which restricts the habitat that is available for reproduction. In the case of the Glanville fritillary, the host plants are *Plantago lanceolata* and *Veronica spicata,* which are uncommon species in Finland except in the Åland Islands in the northern Baltic, between southwest mainland Finland and Sweden. In this part of Northern Europe, the bedrock is made up of volcanic

Fig. 8.2 The Glanville fritillary butterfly *(Melitaea cinxia)*. (Photograph courtesy of Thomas Delahaye)

rocks formed more than 1700 million years ago. Following land uplift since the last glacial period, the landscape is a small-scale mosaic of granite outcrops and intervening areas with sedimentary deposits supporting forests and, presently, small cultivated areas. Roughly 1 % of the land area in the Åland Islands is covered by small dry meadows, often on rocky outcrops. The Åland landscape is a perfect example of a highly fragmented landscape, with 4000 small meadows within the total area of 50 by 70 km. Most of the meadow habitat occurs on the main Åland island, not on the numerous surrounding small islands, and hence the setting is not an archipelago of true islands but a huge network of habitat islands. The meadows are typically much smaller than 1 ha in area (median 0.17 ha), and none is greater than 10 ha (Ojanen et al. 2013). In the beginning, I did not know about the 4000 meadows, I had only a most vague idea of the occurrence of the butterfly. But I was soon to find out much more. In the spring of 1991, I sent two undergraduates, who later became my first postgraduate students, Mikko Kuussaari and Marko Nieminen, to Åland to search for post-diapause caterpillars. I asked them to go to one particular area, where based on the information from two lepidopterists the Glanville fritillary had been seen in the late 1980s. And indeed, Mikko and Marko found a large population with thousands of caterpillars. That was good news, and we moved on to the next stage in our plans and conducted a mark-recapture study in June 1991 within a small network of 50 meadows, including the meadow where large numbers of caterpillars had been seen in late April. Based on this work, reported in the journal *Ecology* (Hanski et al. 1994), there were nearly 10,000 adult butterflies in this network. We recorded frequent movements of butterflies among the small populations, local extinctions and colonizations and other features matching the assumptions of the models—we had found a real metapopulation! I had my wife and my 4-month-old son accompanying me in the field.

From this first piece of fieldwork in 1991, the Glanville fritillary project has evolved into a very substantial research enterprise. Starting from 1993, we have mapped and surveyed the entire 4000 meadow network (Fig. 8.3), perhaps the largest patch network for any species studied in detail that we have done in the case of the Glanville fritillary. In any one year, 500–800 meadows have had a breeding population based on the presence of caterpillars in late summer (Hanski 2011), when the entire patch network has been surveyed with the help of a small army of 50–60 undergraduate students. With that many field assistants, the survey takes 2 weeks, during which every meadow is visited and the relatively conspicuous larval webs are counted (Fig. 8.3). The web is a critical feature of the butterfly's natural history for us researchers: Were the larvae solitary, the large-scale survey would be entirely impractical. The function of the web to caterpillars has remained uncertain. It does not seem to provide efficient protection against a specialist braconid parasitoid, but it may help keep the full-sib caterpillars together. The compact web which the caterpillars spin for the winter and inside which they diapause may be important in preventing dehydration during the long winter. In spring, the caterpillars are black with red heads, warning generalist predators of their bad taste, which they have acquired by sequestering iridoid glycosides from the host plants. The black colour

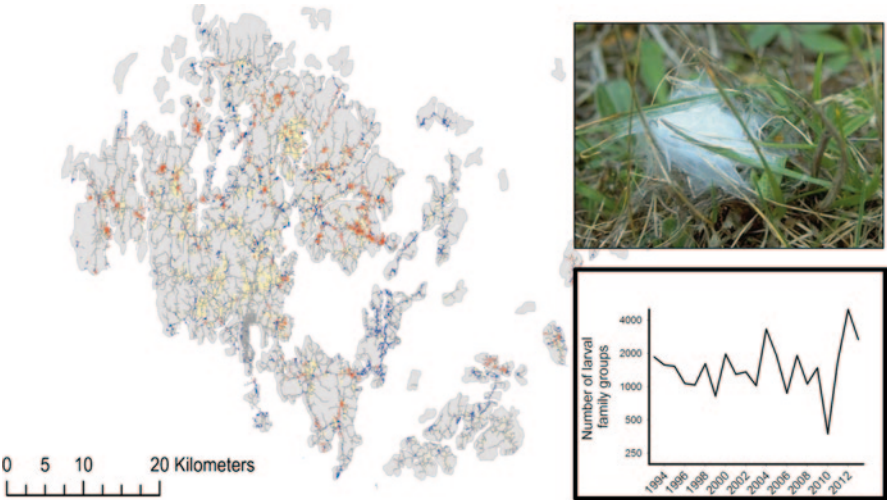


Fig. 8.3 A map of the Åland Islands. The small *red* and *blue dots* indicate dry meadows that were occupied and unoccupied in 2011, respectively. The map also shows cultivated areas *(yellow colour)* and roads. The meadows are typically clustered around small villages. The photograph shows a larval winter web inside which the group of full-sib larvae diapause. The web is white and quite conspicuous in early September, when the Åland-wide survey is carried out. The graph shows a time series of the number of larval family groups in the metapopulation for the years 1993–2013. To have comparable figures, this graph shows the results for about 1600 meadows that have been surveyed systematically since 1993. Notice that the vertical axis is logarithmic. There is no increasing nor decreasing trend in metapopulation size, but the amplitude of fluctuations has increased over the years, reflecting the increasing frequency of dry weather in July, a critical period for pre-diapause caterpillars. This is another likely consequence of climate change

is helpful while the caterpillars bask in the sun to raise their body temperature far beyond the ambient air temperature during cool days in April.

Thousands of Extinctions, and One Other Population Struggling to Survive

Out of the 500–800 local populations that have existed in each year, a large fraction, of the order of 100 populations, has gone extinct per year, the exact number varying from 1 year to another depending on, for example, weather conditions. During dry summers, the host plants tend to wither in July and the caterpillars starve. For this reason, though adult butterflies would benefit from sunny weather, substantial rainfall in early summer is very important for the survival of their offspring. Other causes of local extinction apart from starvation due to dry weather include parasitism by a specialist braconid parasitoid (Lei and Hanski 1997). When this happens, the local parasitoid population will also go extinct, as the parasitoid is strictly specialized to the Glanville fritillary, but some host and parasitoid individuals may have dispersed to nearby other meadows, and hence the interaction persists in spite of local extinctions, in a true metapopulation fashion. I have discussed elsewhere several other causes of extinction, operating either in local populations or at the level of the entire metapopulation (Hanski 1998).

I have already explained that Professor Suomalainen presumed that the final demise of *H. lycaon* from Finland in the 1930s was due to reduced genetic variation in the small dwindling populations. Our research on the Glanville fritillary has confirmed that inbreeding in small populations indeed increases their risk of extinction (Saccheri et al. 1998). There is also another interesting connection between Professor Esko Suomalainen, small populations and the Glanville fritillary itself. Esko Suomalainen's brother, Heikki Suomalainen, was a keen naturalist and lepidopterist before becoming a biochemist. In the summer of 1936, the same year when *H. lycaon* went extinct from Finland, Heikki Suomalainen collected butterflies on the islands in the Gulf of Finland, including a very small island called Pikku Tytärsaari (PT), where he found the Glanville fritillary. The PT island has never been inhabited by people, but it was frequently visited by fishermen and others, often travelling from the Estonian coast, and we have good reasons to believe that caterpillars of the Glanville fritillary were accidentally introduced to the island (Mattila et al. 2012). After the war, this island remained behind the new border, in Russia. In 1993, a joint Russian-Finnish biological expedition was organized to the islands, including PT, where the Glanville fritillary was found to still persist. I heard about this, and I became very excited. The PT island has just a single shore line meadow, about 10 ha in area, and the island is very isolated, 30 km from the Estonian coast and an even longer distance from the nearest areas where Glanville fritillary populations might occur. PT is an ideal contrast with the large 4000-meadow network in the Åland Islands. The only problem was access. The island is located in the border zone, and hard as I tried, I could not find a way of getting a permit for a visit. Finally, in 2009, I made contact with a Russian botanist working on the islands in the Gulf of Finland, and we arranged for her to go and check whether the butterfly would still occur on the island, and if yes, to collect a sample of caterpillars. The butterfly was there, and over the next 3 years we conducted a series of studies to find out whether it had become locally adapted, which might have contributed to its long-term persistence in spite of small size and complete isolation. The result was just the opposite; we found that the population had not only greatly reduced genetic variation, as expected, but also greatly reduced fitness in comparison with butterflies from Åland (Mattila et al. 2012). The fact that it still was alive has more to do with good luck than good genes, and clearly the long-term prospects are not good at all. I fear that this very unique population, first discovered by Heikki Suomalainen in 1936, may be an example of what happens to innumerable remnant populations that become left behind by habitat conversion in landscapes dominated by humans.

Recolonizations and Long-Term Viability

In the Åland Islands, frequent local extinctions are compensated for by the establishment of new populations by mated females dispersing to currently unoccupied meadows. Roughly 100 new populations are thus established every year, and the balance between extinctions and recolonizations has remained so close that there has been no increasing or decreasing trend in the size of the metapopulation as a whole during the past 21 years. Nonetheless, the amplitude of fluctuations in the size of the metapopulation has increased over the years (Fig. 8.3), and the dynamics have become increasingly spatially correlated. Our analyses suggest that the culprit is the increasing frequency of dry weather during the critical time of the year, in July, which has caused frequent deep declines in the size of the metapopulation. Fortunately for long-term persistence, the Glanville fritillary has very high fecundity; a female may lay more than 1000 eggs in her lifetime, and hence the metapopulation has been able to bounce back in the following year. Fortunately, two or more bad years have not occurred, so far, in a row.

The Glanville fritillary metapopulation persists in a balance between local extinctions and recolonizations—it is a perfect example of a classic metapopulation. We have shown both with mathematical models (Hanski and Ovaskainen 2000) and with our empirical research that a landscape needs to have a large enough network of habitat patches for the metapopulation to survive (Hanski 2011). If the landscape is below this critical limit, called the extinction threshold, recolonizations are not frequent enough to compensate for the inevitable extinctions of small populations, and sooner or later the entire metapopulation goes extinct. This is the threat that many species living in human-dominated landscapes face: Too little habitat remains, and what remains is too highly fragmented to allow long-term persistence. The challenge for our research has been to quantify what, exactly, is "too little habitat" and what is "too highly fragmented". The results from the long-term study of the Glanville fritillary have important implications for conservation of species and of biodiversity, which we have elaborated in dozens of original articles, book chapters and books (Hanski 2005).

Moving to the Genomic Era

Most recently, our research has moved on to integrate molecular biology and genomics with our long-term ecological research. We have sequenced the full genome of the Glanville fritillary (Ahola et al. 2014), and it has thereby joined the ranks of those two other butterfly species whose genomes are known, *Heliconius melpomene* and the Monarch butterfly, *Danaus plexippus*. We now have knowledge of thousands of genes and of variation in these genes, which can be related to variation in life history traits and measures of individual performance. The hope is to establish molecular-level understanding of the processes that ultimately play out at the landscape level to determine the viability of species in fragmented landscapes. One process of particular importance is flight, which is critical for anything that butterflies do. We have measured the flight metabolic rate, by measuring the rate of CO_2 emission of butterflies flying in a small metabolic chamber. On the one hand, we have documented changes in gene expression following flight, and on the other hand, we have shown that butterflies with higher flight metabolic rate disperse longer distances in the field. This type of merging of research from molecules to the organism, and to metapopulations at the landscape level, is very exciting.

Having sequenced the full genome of the Glanville fritillary, we have found another interesting link between Professor Esko Suomalainen's research and our work on the Glanville fritillary. Suomalainen, who worked among other things on chromosome evolution, suggested in 1969 that the ancestral chromosome number in Lepidoptera is 31 (Suomalainen 1969). With the genome and a high-density linkage map for the Glanville fritillary, which happens to have 31 chromosomes, we have been able to confirm Suomalainen's conjecture: The ancestral lepidopteran karyotype has indeed $n = 31$, and this karyotype has been retained for at least 140 million years in some clades of butterflies and moths, though most extant species have different chromosome numbers, mostly due to chromosome fusions. This finding raises new questions about genomic architecture—is there something special about the genomes of Lepidoptera that we have not yet discovered?

Web of Lepidopterists and Expanding Knowledge

Reflecting back on the two most important butterfly species in my life, the dusky meadow brown and the Glanville fritillary, makes me realize what good luck and life I have had. I might have become a biologist without the dusky meadow brown, but I might not; the female specimen that I encountered in my childhood led to such a chain of events that my destiny was set. The Glanville fritillary has helped establish and consolidate the field of metapopulation biology, for which this butterfly is now well known. Through these two butterfly species, my work has become entwined with the work of many other lepidopterists. My research on the Glanville fritillary has touched upon important questions that Professor Suomalainen asked about the dusky meadow brown half a century ago, including the consequences of reduced genetic variation in small populations. My research on the Glanville fritillary was stimulated by Paul Ehrlich's pioneering work on Edith's Checkerspot in a system of three meadows at Jasper Ridge, and, as I have explained in this essay, I might not have selected the Glanville fritillary as my study system in 1991 without Paul's work. I am particularly glad that I had an opportunity to edit a volume on the biology of checkerspot butterflies with Paul (Ehrlich and Hanski 2004), which brought together our results on the American and European species up to 2004. Paul was awarded the Crafoord Prize for his work in 1990, and I received the same honour in 2011. I like to think that our two butterfly species were also honoured, along with all our students and associates. I have had the privilege to collaborate with Michael Singer, Paul's former student, and with Chris Thomas, Michael's former student, both amazing lepidopterists of their own special kind. There are other such links, but this example suffices to demonstrate the kind of web we belong to, and the context in which we do our best to advance knowledge, building upon the achievements of our predecessors.

References

Ahola V, Lehtonen R, Somervuo P et al (2014) The Glanville fritillary genome retains an ancient karyotype and reveals selective chromosomal fusions in Lepidoptera. Nat Commun 5:4737. doi:10.1037/ncomms5737

Ehrlich PR (1965) The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. Evolution 19:327–336

Ehrlich P, Hanski I (eds) (2004) On the wings of checkerspots: a model system for population biology. Oxford University Press, New York

Gyllenberg M, Hanski I (1992) Single-species metapopulation dynamics: a structured model. Theor Popul Biol 42:35–61

Hanski I (1983) Coexistence of competitors in patchy environment. Ecology 64:493–500

Hanski I (1989) Metapopulation dynamics: does it help to have more of the same? Trends Ecol Evol 4:113–114

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hanski I (2005) The shrinking world: ecological consequences of habitat loss. International Ecology Institute, Oldendorf

Hanski I (2011) Eco-evolutionary spatial dynamics in the Glanville fritillary butterfly. Proc Natl Acad Sci U S A 108:14397–14404

Hanski I, Gyllenberg M (1993) Two general metapopulation models and the core-satellite species hypothesis. Am Nat 142:17–41

Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. Nature 404:755–758

Hanski I, Kuussaari M, Nieminen M (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762

Langer TW 1961. Päiväperhosten parissa. Werner Söderström, Porvoo

Lei G, Hanski I (1997) Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. Oikos 78:91–100

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Levins R (1970) Extinction. Lect Notes Math 2:75–107

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Marttila O, Haahtela T, Aarnio H, Ojalainen P (1990) Suomen päiväperhoset. Kirjayhtymä, Helsinki

Mattila ALK, Duplouy A, Kirjokangas M, Lehtonen R, Rastas P, Hanski I (2012) High genetic load in an old isolated butterfly population. Proc Natl Acad Sci U S A 109:E2496–E2505

Ojanen S, Nieminen M, Meyke E, Pöyry J, Hanski I (2013) Long-term metapopulation study of the Glanville fritillary butterfly (*Melitaea cinxia*): survey methods, data management, and long-term population trends. Ecol Evol. doi:10.1002/ece3.733

Saccheri IJ, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. Nature 392:491–494

Suomalainen E (1958) Über das Vorkommen und spatere Verschwinden von *Epinephele lycaon* Rott. Lep., Satyridae in Finnland. Ann Entomol Fenn 24:168–181

Suomalainen E (1969) Chromosome evolution in the Lepidoptera. Chromosome Today 2:132

Ilkka Hanski is professor of ecology in the University of Helsinki since 1993, research professor since 1996, and the director of the Metapopulation Research Centre since 1991. He has DPhil in Zoology from the University of Oxford (1979). Hanski established the new field of metapopulation biology with a series of papers, books and edited volumes in the late 1980s and the early 1990s. Metapopulation biology is concerned with the biology of spatially structured populations, including the ecological, genetic and evolutionary consequences of natural and anthropogenic loss and fragmentation of habitats. Hanski is an elected member of many science academies, including the Royal Society and the National Academy of Sciences (USA). He has served in many scientific advisory bodies and agencies, including the European Research Council, the European Academies, the Advisory Board of the UK Population Biology Network and the SAB of the National Center for Ecological Analysis and Synthesis in Santa Barbara, USA. He has received numerous prizes and awards, including the Crafoord Prize, the Latsis Prize and the Balzan Prize.

Chapter 9
Tropical Caterpillar Addiction

Annette Aiello

It's tempting to begin this account with "It was a dark and stormy" journey to the Lepidoptera, but I will resist. It's true though that the path was a long and convoluted one, with plenty of possibilities unrecognized and opportunities missed.

I was born in 1941 in a large city, New York. We lived in Brooklyn, where the neighbors' yard held the only nearby representative of the natural world, a magnificent magnolia tree. The flowers and their perfume were the most wonderful things imaginable. I collected fallen petals in a shoe box and a few days later suffered a great disappointment when the petals turned brown.

My earliest encounter with nature was my grandmother's garden in Guilford, CT. It was simply gorgeous. On visits there, from toddler years on, I spent hours making the rounds of every plant in that garden. It had all the elements one might expect in a garden of that era: irises, lilies, roses, a rock garden with *Opuntia* cactus and *Portulaca*, *Gaillardia*, *Hosta*, love-in-a-mist *(Nigella damascena)*, mullein-pink *(Silene coronaria)*, snowberry *(Symphoricarpos albus)*, and nasturtium *(Tropaeolum majus)*; and of course, lots of butterflies. Children are naturally attracted to flowers and butterflies, and they feel a powerful urge to interact with them but don't know how. I remember that "Don't touch" frustration well (Fig. 9.1).

In 1948, my family moved to Killingworth, CT, a rural town where houses were few and far between, and where I attended a one-room schoolhouse. Now we were surrounded by nature. Killingworth then was mostly woodland, abandoned fields, small streams, swamps, and cranberry bogs, and I explored these at every opportunity, year round. I collected bird nests, shed snakeskins, rocks, and shells. And I raised and released baby birds that fell from their nests. In those days, before widespread light pollution and the rampant use of dichlorodiphenyltrichloroethane (DDT), the windows on summer evenings were teeming with insects, especially large colorful moths. As with the magnolia petals, I felt compelled to collect them. Having no guidance as to procedures or equipment, I dispatched them with carbon

A. Aiello (✉)
Smithsonian Tropical Research Institute, Ancon, Balboa, Republic of Panama
e-mail: aielloa@si.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_9

Fig. 9.1 Don't touch! The author conversing with flowers, July 1942, Guilford, CT

tetrachloride and displayed them in windowed handkerchief boxes lined with milkweed down. Of course, after a few years of labor by museum pests, the milkweed down was all that remained.

During my early teen years, a neighbor took me along on Connecticut Botanical Society field trips. They were wonderful, but I didn't know that one could study plants and animals in any formal way and make a career from something they liked to do. It took decades for me to figure that out. It was no help that high school biology was quite dull, except that I had a crush on the teacher. The course was taught entirely from a textbook with no laboratory sessions or field trips at all. If anyone had predicted then that I'd eventually do a PhD thesis in botany or go on to study insects, I would have said "Very funny." On top of that, the results of a "general interest" survey administered in our senior year (1959) were interpreted to suggest that I take up a career as a flower arranger.

I left home right after high school graduation and returned to New York City to study music. Once again I was severed from nature. I supported myself with a series of jobs: painting fingernails at a manikin factory in the garment district, working in a shoe factory in Greenwich Village, and coding questionnaires at the American Cancer Society.

Later, I moved to New Orleans for a few years and worked in a department store's accounting department and later was the jewelry-receiving clerk in Adler's jewelry store, a truly fun job as one never knew what wonders a package would hold. On the music side, I sang in the local orchestra chorus and the opera chorus. Throughout my years in New Orleans, I was intrigued by the plants, insects, and birds there, and though I passed the natural history museum on my bicycle ride to work every day, and though I thought of stopping in there to ask questions, I didn't do it. The museum opened after my working hours began and closed before they ended. Why didn't I call in sick and just go there? A combination of shyness and job responsibility most likely. Among the opportunities missed, that one perhaps was the most lamentable as it had the potential to point my life in the right direction almost instantly.

On my return to New York, I worked at the Diner's Club accounting office, then a feature news agency, and then Basic Systems Inc. (a now defunct subsidiary of the Xerox Corporation). Clearly, I needed to identify and focus on a meaningful career. But what? Why biology wasn't obvious I'll never know. A newspaper ad led me to the Germaine School of Photography, located in the basement of the Transportation Building in Lower Manhattan. The course was intensive, a 600-h curriculum covering every aspect of commercial black and white photography. Mainly we used large format studio cameras—with 5″ × 7″ sheet film. We lugged them and their huge tripods around on public transportation to reach our various field assignments, which included the construction sites of the World Trade Center and Lincoln Center. When the course ended in May 1967, I got my first camera, a Nikon single-lens reflex. It was spring, and instead of continuing exclusively in black-and-white format, I found myself taking hundreds of photographs of plants and insects. I photographed weeds in abandoned lots and railroad beds in the Brooklyn Bridge area, and wild flowers and insects all over the place in Connecticut where mother drove me around on weekends. A Killingworth neighbor invited me to go botanizing. She told me about a book called *Gray's Manual of Botany* that covered all the New England plants. I bought a copy and spent the next winter learning the terminology and trying to identify the plants in my photographs. It was beginning to sink in that biology could give my life meaning.

Finally, at the age of 28, I realized it was time to go to college. I majored in biology at Brooklyn College, and then went on to the Graduate School of Arts and Sciences at Harvard University. My doctoral thesis took me to Jamaica and Mexico, and it was in Jamaica that insects began to attract me greatly. I was especially intrigued by a treehopper (Membracidae) that had a colorful bubble-like projection which it threw off with a snapping sound when disturbed; I've never seen such a bizarre insect since. My guide in Jamaica was kind enough not to inform my Harvard advisor that I was collecting insects in addition to the thesis plants.

In 1976, as I was finishing the thesis, unexpected life events diverted me to Barro Colorado Island (BCI) Panama (Fig. 9.2) for 6 months a year to collaborate on a butterfly project with Robert Silberglied, a Harvard professor in entomology. Until his death in early 1982, we spent each March–August in Panama studying the two commonest butterflies in the neotropics, *Anartia fatima* of Mexico and Central America, and *Anartia amathea* of South America. We learned that they hybridize in Panama's Darien Province, towards the Colombian border (Fig. 9.3). Did they mate at random, or did they choose mates? What were the consequences of hybridization? Why didn't the two species spread into each other's ranges? To investigate those and other questions, we raised hundreds of butterflies for mate choice tests. Our waking hours were consumed with capturing females and harvesting eggs from

Fig. 9.2 Barro Colorado, Panama. *Upper left:* Approaching the dock from Gatun Lake. *Lower left:* Ascending the more than 100 steps from the dock to the Dining Hall and dormitory. *Upper right:* Barbour House, where we lived and conducted laboratory research. *Lower right:* The Herbarium, with a spider monkey and baby on roof

them, collecting caterpillar food plant, feeding caterpillars, separating pupae as they formed, marking adults individually as they emerged from their pupae, feeding adults, running the mate choice experiments, and keeping meticulous records of every individual for several generations. The caterpillar food plant was an abundant weed, *Blechum pyramidale* of the family Acanthaceae. To feed so many caterpillars, we had to travel off-island and collect huge amounts of *Blechum* along roadsides and waste areas, about a dozen garbage bags full per week. The project was intense

Fig. 9.3 *Anartia fatima (left), FA* hybrid *(middle), Anartia amathea (right)* (family Nymphalidae)

and unrelenting, and we were slaves to it, 18 h per day, 7 days a week. As each generation of caterpillars grew to their largest size and approached pupation, they became voracious and we nearly went crazy trying to keep up with feeding them and cleaning their little cages, which were made from window screen cylinders with Petri dish bottoms and covers, and which held 25 caterpillars apiece. We sent 15 pounds of caterpillar fecula per week to a biologist in town, who used it as orchid fertilizer.

As the result of our efforts, we learned that the initial hybrids between the two species are healthy. We called them *AF* and *FA*. *AF* stands for an *amathea* female mating with a *fatima* male, and as you might guess, *FA* stands for a *fatima* female mating with an *amathea* male. Though the wing patterns of the two hybrids were more or less intermediate between the two species, they were not identical. Not only that, but their behaviors were quite different. Though *FA* females mated readily, *AF* females resisted mating with anyone, and even when they did mate, most of their offspring died as tiny hatchling caterpillars. Thus, genetic incompatibility helped keep the two species apart.

In addition to the initial hybrids, we did 12 other crosses between the two species, and that involved rearing the butterflies through three or sometimes four generations and obtaining the complete genealogy for each individual. With these crosses, we saw further breakdown in their ability to reproduce successfully. The 12 crosses were: four second-generation crosses among the hybrids: *AF*/*AF*, *AF*/*FA*, *FA*/*FA*, and *FA*/*AF*; and eight back-crosses between the hybrids and the original species: *A*/*AF*, *A*/*FA*, *AF*/*A*, *FA*/*A*, *F*/*AF*, *F*/*FA*, *AF*/*F*, and *FA*/*F*. The butterfly specimens from this study are housed in the collection of the Museum of Comparative Zoology at Harvard.

You have to be young and slightly nuts to undertake such a large rearing project, and I do not recommend it to anyone unless they already are quite mad and/or have lots of helpers. In spite of it all, I still enjoy seeing *Anartia fatima* fly by, and always I say a fond “Hello.”

The two main creatures on our walls in Barbour House on BCI were the large native forest gecko, *Thecadactylus rapicaudus*, and the common American roach, *Periplaneta americana*. Our first impulse was to squash the roaches, but, instead, we decided to put names on them. We painted white typewriter correction fluid on the large plate (pronotum) that covers the thorax, and when that dried, we used a fine technical pen to write names: Alice, Elmer, Harry, etc. It was quite a surprise to discover that there were only six individuals, not millions, and a further surprise to learn that once we thought of them as individuals, our attitude toward them changed completely. They came and went and we worried about them when one was absent for more than a few days. We put up two silly signs: “Please do not kill the roaches, the geckos eat them” and “Please do not kill the geckos, they eat the roaches.” Sometimes the roaches travelled to the habitation above, and there Alice was saved from certain death when Andrea Worthington, our upstairs neighbor, noticed the roach she was about to step on had a name. Weeks later, when our new upstairs neighbor was John Pickering, I was awakened one night by a scratching sound. Approaching cautiously with a flashlight, I discovered the source: a roach chewing the binding of a notebook. It had a name. Who was it? Closer now, I read “Hi Bob and Annette,” and a smiley face. John had found an unmarked roach and had been waiting two weeks for us to see it. Luckily, I got that opportunity, because it was never seen again.

It was on BCI that I fell in love at first sight with tropical caterpillars in general. The botanical thesis did get finished and published, but caterpillars put an end to my formal connection to botany. The thesis wasn’t wasted time and effort, however. My botanical knowledge served me well because, after all, caterpillars eat plants. BCI was a biologists’ paradise. It was brimming with life and thanks to the forest guards, who patrol the island 24 h a day on foot and by boat, it was safe to wander the trails even at night to search for caterpillars or gather emergency food plant. Meals on BCI were, and still are, cafeteria style. There was no food shopping, cooking, or washing dishes. Back then, unlike now, there were no telephones on the island. And, of course, it was before e-mail or even computers. Life was simple: eat, sleep, work.

At that time, most tropical caterpillars had not yet been associated with their adults, and I quickly became addicted to rearing them to find out who they were and how they lived; quite reminiscent of opening packages at Adler’s, only much more exciting. Dan Janzen and Winnie Hallwachs were just beginning their massive Lepidoptera rearings in Costa Rica, and Diomedes Quintero was starting the insect collection at the Universidad de Panamá. These were some of the best years of my life.

One of the first creatures to arouse my curiosity was not large or colorful. It was the maker of the small sand and silk cases (Fig. 9.4) that adorned the walls of the BCI buildings inside and out. They were half-inch long, spindle shaped, and flattened, and each contained a larva that stuck out one end and pulled the case behind it. I say “larva,” not “caterpillar,” because I didn’t know what these little guys were, or what they were eating. Were they moths? Beetles? Flies? Some weird worm? Nobody on BCI could tell me. In Barbour House, where we stayed, there were lots of them in the bathroom, and I did a mark-recapture study of the cases in there to find out where individuals went, how far they moved, and when they were active. Liquid paper painted on a small area of each case provided a background to write individual numbers using a 000-pen. I captured larvae from the other buildings to study them in captivity and, as they developed, provided them with different colored particles (white sand, black sand, powdered red brick) to observe the case-making sequence. I could hardly sleep thinking up things to try with them. I installed windows by cutting a square hole in a few cases and gluing a piece of plastic wrap over the opening to see what went on inside. The larvae were most active at night. They were eating animal hair and dead insects, and turned out to be clothes moth relatives. I dubbed them “bathroom moths.” They stacked their food neatly inside the case. They turned around inside the case by doubling back on themselves in the wide, center portion. I followed them from egg to adult, feeding them dead mosquitoes, which they liked very much, and I even managed to get a number of them through on a diet of my hair alone. I found that in order to be nutritious the hair had to be dirty, which meant going several months without washing my hair. The findings formed my first single-author entomology paper, *Life history*

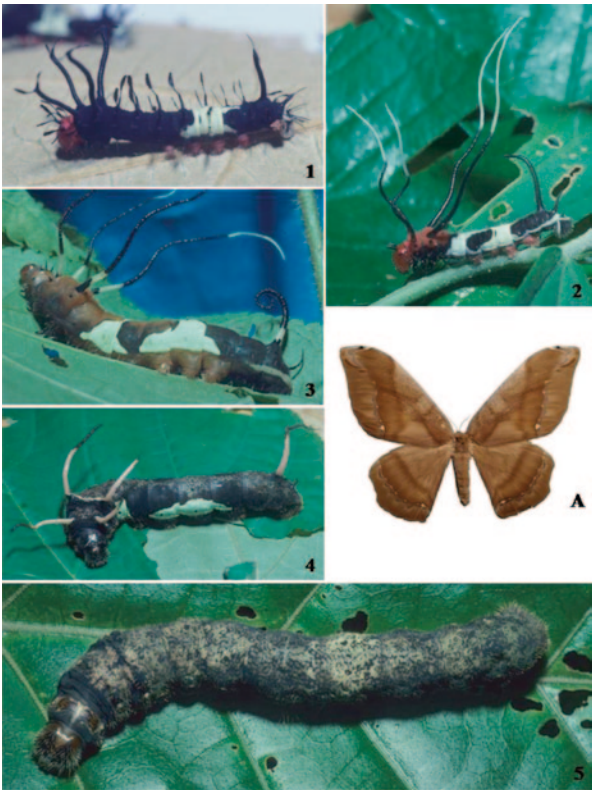
Fig. 9.4 The bathroom moth (*Phereoeca allutella*, Tineidae). Clockwise from *upper left:* an accumulation of pupation cases in a corner; a case partially cut open to show the larva and its larder, my hair; the case of a larva that was provided with different colors of building materials during its development; two cases with windows; case number 23; an adult moth; a larva reaching out of its case to pull a mosquito inside

and behavior of the case-bearer Phereoeca allutella (Rebel, 1892) (Tineidae). It seems appropriate to end this account of the bathroom moth with its motto, “Hair today, guano tomorrow.”

Anyone who has reared insects has experienced sleepless nights of anticipation prior to emergence of the adult of an unidentified species. For me, the most difficult waits occurred when I had some idea what the moth or butterfly might be. Those outcomes were a rewarding combination of confirmation and surprise. The anticipation was especially acute when rearing butterflies of the genus *Adelpha* Hübner, [1819] (Nymphalidae). *Adelpha* is special because, as I discovered, the keys to understanding the evolutionary relationships among its 85 species lie in the forms of the caterpillars and pupae. Their adult wing patterns do not reflect species relationships. Species with similar patterns often are unrelated, and related ones often look quite different from one another. It is not known why that is, but it is so.

Of the 36 species of *Adelpha* known in Panama, I have reared 14. Well, actually only 13. The 14th one fell into my hands on three occasions, in 1982, 1983, and 1985, and each time it died, twice as a caterpillar, and once as a pupa just a day before expected eclosion. Please, readers, would one of you find and rear this frustrating creature, which I have dubbed *Adelpha croaki*. It eats the leaves of a tree called *Heliocarpus* (family Malvaceae), and it belongs to the *Adelpha serpa* group.

Fig. 9.5 *Arsenura batesii* (family Saturniidae). *Numbers* correspond to caterpillar stages *1–5*. *A* adult



There is reason to suspect that it will turn out to be *Adelpha radiata aiellae*, but we just don't know (Keith Willmott, personal communication).

Failed rearings are discouraging, but there is always hope for another opportunity, though sometimes it takes years to get an answer. It is amazing how the mind can accumulate hundreds of isolated observations and retain them for decades, ready to fit into place when a new observation or insight presents itself. As an example, because the caterpillars died because of a variety of mishaps, it took some time to realize that several rather different-looking ones (Fig. 9.5) represented different larval stadia of the same species, *Arsenura batesii*.

Over the years, I learned that many other species of Lepidoptera have caterpillars that change in form or pattern as they develop (Fig. 9.6). The butterfly *Dynastor darius* (Fig. 9.6D) has three different head forms during its life. When the caterpillar emerges from the egg, it is tiny; the body blends with the leaf, and the fuzzy head looks like a bit of mold. When it molts (sheds its skin), the intermediate stages have smooth heads protected by horns and have a complex pattern of triangles. In the final stage, the caterpillar has a brown head with black horns and black border. The pupa is spectacular; it resembles the head of a snake. I had a number of these pupae suspended in their little cages on my work table, and whenever the table

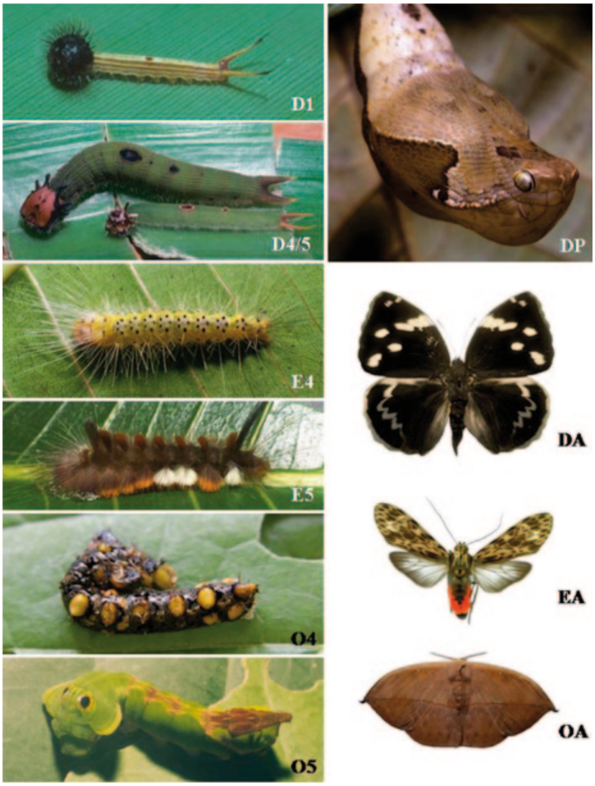


Fig. 9.6 Three species whose caterpillars change their appearance as they develop. *D* = *Dynastor darius* (family Nymphalidae); note that the pupa closely resembles the head of a snake. *E* = *Eucereon latifascia* (family Erebidae). *O* = *Oxytenis modestia* (family Saturniidae). Numbers correspond to caterpillar stages. *P* pupa. *A* adult

jiggled enough to disturb them, they thrashed side to side, triggering my adrenaline every time. Another example of change in appearance with development is the moth *Eucereon latifascia* (Fig. 9.6E). The caterpillar is yellow with tiny black spots and sparse beige setae (hairs), but when it molts to the final stage, its appearance changes dramatically. It bowled me over when it molted because I had collected both forms, never imagining that they pertained to the same little moth. An interesting twist to the complexity of caterpillar form is that there are many examples of totally unrelated species that are similar in form and/or color pattern (Fig. 9.7).

Evolution has produced myriad caterpillar defense strategies: concealment, camouflage, imitation of inedible objects, false threatening eyes, toxins, poisonous spines. Each of these strategies has endless variations and can change each time the caterpillar molts. It is such fun to be fooled and then discover that what you thought was inanimate really is a caterpillar. The moth *Oxytenis modestia* (Fig. 9.6O) had several surprises for me. The caterpillars rested curved on their food leaf and resembled bird droppings with seeds in them. But when they molted to their final stage, they were green or brown, and the thorax had false eyes that they could open and close by inflating or deflating the body using blood pressure. When disturbed, they opened the eyes and reared up, waving back and forth like a snake. The adults rested with the wings flat and spread to closely resemble dead leaves, and when

Fig. 9.7 Three pairs of unrelated caterpillars that have similar color patterns and/or forms. *Top row: left:* a moth, *Oxytenis naemia* (Oxytenidae), and *right:* a butterfly, *Adelpha phylaca pseudaethalia* (Nymphalidae). *Middle row: left:* a moth, *Pseudodirphia eupanamensis* (Saturniidae), and *right:* a butterfly, *Hamadryas iphthime* (Nymphalidae). *Bottom row:* two unrelated moths: *left: Mesoscia dumila* (Megalopygidae) and *right: Apatelodes paratima* (Apatelodidae)

touched, they wafted to the ground just like fallen leaves, never moving the wings at all.

Meanwhile, back at *Adelpha*, another rearing that took a stressful turn several days before the adult was to emerge had a happy ending. The USA invaded Panama and toppled the dictatorship, and the highway to the city was closed for 1 week. Without periodic ventilation and humidity monitoring, most of the pupae in my lab were doomed. The *Adelpha* was of particular concern because it belonged to a species I had not reared before and had only one individual of. Once the highway reopened, we made a beeline for the city. All of the pupae had failed, with one exception, the *Adelpha*. The adult had emerged flawlessly and died on the cage floor with the wings perfectly spread. It was *Adelpha messana messana*, known to me at that time as *Adelpha ixia leucas*, which was the name used in my publication about it.

Sometimes, caterpillars survive a series of misfortunes against all odds. Such was the case with a large owl butterfly caterpillar, *Caligo idomeneus*, that was brought to me with no food plant, with parasitic fly eggs stuck all over its head, and with an internal thoracic rupture incurred when it landed on someone's shoulder and suffered a reflexive whack. Not having any idea what this intriguing caterpillar was, I used forceps to remove the fly eggs—luckily not yet hatched—and offered it a salad of every plant around; it chose *Heliconia latispatha*. Being asymmetrical because of the rupture, the caterpillar did not attach well to its support, and it fell soon after pupation, while still soft. Now the pupa was flattened on one side and almost certainly done for. Incredibly, it endured and reached the adult stage, though the wings are noticeably larger on one side than the other.

Many biologists suffer spectacular accidents in the field, but I am sorry to disappoint the reader. Despite several close calls, I have had no serious falls or adventures and no broken bones, just two relatively minor, but miserable mishaps. The first was an attack by a female wandering spider, *Phoneutria boliviensis* (family Ctenidae) who, unknown to me, was guarding her egg sac a few feet away in the same tree I was collecting a leaf from. When I jiggled the branch, she rushed over, bit my right ring finger then dropped to the leaf litter and raced away. She was quite large; the fang marks were 8 mm apart. The pain was excruciating and lasted 12 h, during which time I was unable to work, or eat, or escape by sleeping. Wandering spiders are especially common in banana plantations and are the misnamed "tarantulas" of the "Banana Boat" song.

The other incident had to do with ticks. BCI is famous for ticks, and their removal is part of one's evening ritual. Ticks are not nearly as common in Arraiján, the little town where we now live, but there they do carry rickettsial diseases (mainly *Ehrlichia* and *Babesia*) that mostly affect cattle and doggies. In July 2003, I contracted *Ehrlichiosis* from a dog tick. The disease began to manifest itself a week or two later during visits to my family in Killingworth and the Smithsonian natural history museum in Washington, DC. Mild flu-like symptoms gradually worsened over a period of a week, giving way to nausea, chills, fever, extreme weakness and total loss of appetite, a horrible headache, and brown vision that made it impossible to see the paperwork I had to sign when admitted to a Washington hospital for four nights. Doxycycline put a stop to the infection, but it was another week before I gained enough strength to return to Panama. Do I now use repellant? Nope. The idea of years of daily chemical applications scares me lots more than a possible rickettsial incident that now I would recognize the symptoms of and seek earlier treatment for. Accidents and the threat of tropical diseases do not deter the field biologist. The allure of what wonders might lie over the next hill or around the next bend is just too strong. Biology is a way of life, not a job. It is an extension of one's self.

The reader who asks "What does any of this have to do with serious science or how does it help society?" has a valid question. Are not biologists just playing, especially when they actually enjoy their work? To understand why our activities are important, try and imagine that you and your family have just landed on an alien planet. You emerge from your spaceship and look around at the strange organisms surrounding you. What are they? Are any of them plants—organisms that derive their sustenance from a combination of earth, air, and energy from their sun? Which animals are dangerous? Which can be eaten? How do all these organisms interact with each other? In other words, you would have all the same questions we have been asking here on Earth for thousands of years. Whatever little details we can discover about life on Earth are important. What a single person contributes may seem like trivial anecdotes, but when woven into the total fabric of our knowledge, a big picture emerges, and it grows slowly but steadily to reveal the vast truth of how life began and perpetuated itself and how the web of life developed its almost unimaginable complexity, which now is being destroyed. And that includes ourselves because we are an intrinsic part of the web. Once our place in it becomes too overbearing, it will all tumble down. But, not to worry. Long after we have disappeared, Earth will recover, and the complexity will restore itself, though with plants and animals different from those we see today.

Annette Aiello is a staff scientist in entomology at the Smithsonian Tropical Research Institute in Ancon, Balboa, Panama, where she has been studying insect life histories for nearly 40 years. Her main focus has been the transformations of moths and butterflies, especially their caterpillars: their development, behavior, and defenses, as well as the clues that they and their host plants can contribute to our understanding of species relationships (classification). Her publications include other subjects as well: plants, beetles, leafhoppers, insect outbreaks, mimicry, and even sloth hair. Her early interests lay in botany, which she pursued on her own until at last entering college in her late 20s. She obtained her BA in biology, magna cum laude, at Brooklyn College in 1972, and an MA and a PhD in biology at Harvard University in 1975 and 1978 respectively. Her PhD thesis was in taxonomic botany: *A Reexamination of Portlandia (Rubiaceae) and Associated Taxa,* with Dr. Richard A. Howard as her advisor. She is a resident of Panama, and she and her Panamanian husband, Ricardo Cortez, live in a small town several miles west of the Panama Canal.

Chapter 10
Tales of Three Tigers: A 50-Year Career-Shaping Journey Chasing Swallowtail Butterflies

Mark Scriber

Having retired (in 2010) as professor emeritus at Michigan State University (MSU), Mark Scriber's time is now spent on recollections of a research career in entomology, with a focus on swallowtail butterflies of the world. For this purpose, a lighthouse was constructed at his family's lakeside home on Waikiki Street in Aloha, MI (Fig. 10.1). Here, the historical and currently emerging aspects of the North American tiger swallowtail butterfly evolution could be continued in retirement (e.g., Scriber 2014; Scriber et al. 2014). According to a local authority (Harold Fox, an 88-year-old neighbor, living in a nearby log cabin), all lighthouses need a name. The name that emerged was "Papa-Leo" (for Grandpa Mark and his birth sign, Leo), which in conjunction is pronounced "Papilio" (the genus of many swallowtail butterflies, including the North American tiger swallowtails). The 3-story, 36-ft high lighthouse was actually a compromise from Mark's lifelong "dream tree-house," largely because the emerald ash borer had just reached these northern Michigan forests and the 120-ft high ash trees in the yard were in serious jeopardy. This construction also put the foundation under his "Castle in the sky…."

Looking back 50 years ago, when his career options were just forming, it was perhaps prophetic that he was cast as "Mr. Papillon" in the 1965 senior play at Hannibal High School. In the play "Rhinoceros" by Eugene Ionesco, Mark needed a large pillow stuffed under his shirt to go with the butterfly net in order to project the proper phenotype of an old lepidopterist. This phenotype later emerged naturally over a few decades as the reality of an academic butterfly-chasing lifestyle unfolded (despite moderate dieting and some serious marathon running). Mark still favors weight-class awards for marathons (for fewer running minutes than initial pounds).

It was also intriguing that his grandfather, DeBlance Scriber, more than 50 years earlier around 1912, created a beautiful beetle-carved wooden serving tray, featuring a tiger swallowtail butterfly from the Adirondack Mountains (Fig. 10.2). This tray was discovered at his Aunt and Uncle Buscall's home near Cambridge, NY, in

M. Scriber (✉)
Michigan State University, East Lansing, MI, USA
e-mail: scriber@msu.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_10

Fig. 10.1 "Castle in the sky…" provides a retirement hangout for Mark. The lighthouse in Aloha, MI, is known as "Papa-Leo" (= Papilio) as a tribute to tiger swallowtail butterflies. Henry David Thoreau said, "If you have built your castles in the air, your work need not be lost: that is where they should be. Now put the foundations under them"…but "what you get by achieving your goals is not as important as what you become achieving your goals"

1999. This *Papilio canadensis* species was what Mark would spend his entire career (with his students) evaluating. As a result of extensive research, this *P. glaucus canadensis* subspecies (Rothschild and Jordan 1906) was eventually and officially elevated to full species status, with *P. glaucus* as its sister species by Mark's research group (Hagen et al. 1991).

Having spent parts of most summers as a child along (and jumping from covered bridges into) the Battenkill River near Cambridge, NY, at his Aunt Betty and Uncle Frank's home, it was especially satisfying that a unique hybrid between these two sister species (*P. glaucus* and *P. canadensis*) was discovered there in July near the Eagleville covered bridge in 1999. Due to his graduate PhD thesis research, Mark knew that individuals of any mid-July "late flight" could not be from a true second generation. As such, these "false-second generation" populations quickly became the subject of intensified studies of hybridization, evolutionary divergence, and temporal reproductive isolation from 1999 to 2013. It was hypothesized that these isolated recombinant hybrid swarm populations were likely incipient "hybrid species" that produced the cryptic species of mountain swallowtail, *P. appalachiensis,* (Pavulaan and Wright 2002). This mountain species turned out to be a hybrid species, which is rare in animals (Scriber and Ording 2005; Ording et al. 2010; Kunte

Fig. 10.2 *Papilio canadensis* from the Adirondack Mountains of New York State was built centrally into a carved wooden serving tray made by Mark's grandfather (DeBlance Scriber) around 1912. This butterfly taxon was elevated from subspecies to full species status in 1991 by Mark and his lab colleagues, and the origins of the "late-flight" and hybrid species *(P. appalachiensis)* was later recognized across the thermally defined hybrid zone of *P. canadensis* and *P. glaucus,* with its center along the historically important Mohawk and Hudson Valleys (Fig. 10.3), where DeBlance was teacher and principal at several different native American Indian schools from 1893 to 1924 with his wife Carrie

et al. 2011). Extensive evolutionary divergence inside the historical hybrid zone in New York and throughout the Appalachian Mountains has been revealed by recent changes in trait clines across geographic transects of the historical hybrid zone. This genetic introgression may have been driven by extensive gene flow after recent climate warming (since 1998) which removed the historical thermal constraints on voltinism patterns (permitting two, rather than one generation annually; Ording et al. 2010; Scriber 2011a).

The Early Years: Inspiration to Become a Lepidopterist

Surprisingly, to Mark at least, it was largely the early impact of his high school English teachers that led to a career in science. Works of transcendentalists such as Henry David Thoreau and Ralph Waldo Emerson blew passion into Mark's love of the world around him and insight for a search for "meaning" in life, through nature. These authors, and another recommended by a different English teacher (*Silent*

Spring by Rachel Carson), kindled an academic fire to drive Mark's 45-year career in this field, seeking alternatives to synthetic pesticides for insect control. During his last summer before senior year in high school, Mark enjoyed a career-clinching experience at the National Science Foundation (NSF)-funded summer camp for high-school kids in "field ecology" at Potsdam University in northern New York, near the Adirondack Mountains (Fig. 10.3). Palmer's *Fieldbook of Natural History* was the course text, but the Adirondack boreal forests and the St. Lawrence River basin were the magnificent classrooms (and his first experience failing to capture a tiger swallowtail butterfly on the wing). Although he fancied himself as an agile athlete, the elusive tiger swallowtail led him awkwardly tripping over streams, slogging through muddy marshes, and stumbling across alpine fields. While this prized specimen never made it into the class insect collection, this summer program

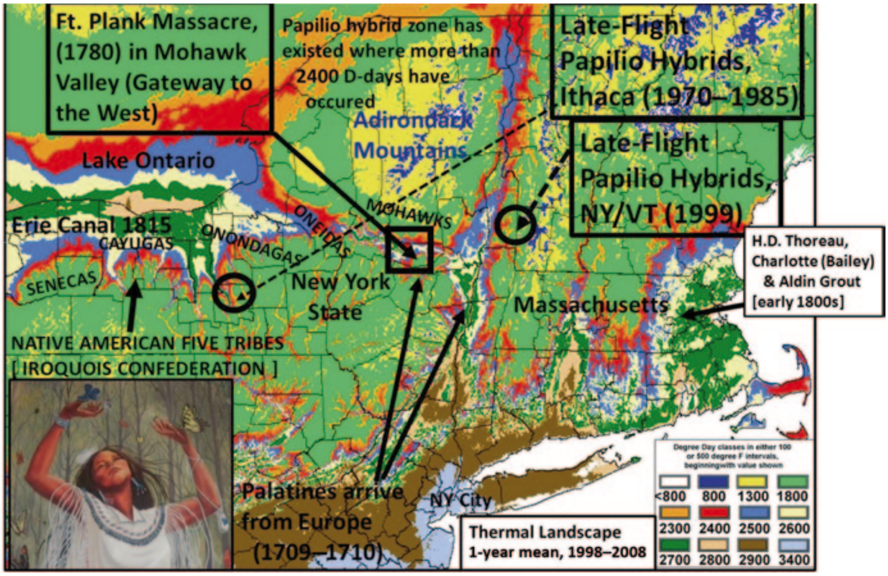


Fig. 10.3 The unique topography and thermal landscape (summer growing degree days) of New York State and surrounding New England areas played an important role in shaping the flora and fauna of the region as well as the human settlements from England and their interactions with native North Americans during the 1600s through 1900. This area was at the center of Mark's academic research as well as his direct ancestors (from the 1709 German Palatines and Albertus Schreiber of Neuweid, near Koblenz, Germany) along the Mohawk River and the Erie Canal in 1815. Not surprisingly, it also was the area that generated the transcendentalists that so deeply impacted Mark's career and life, as well as the "hotbed" of the educational missionaries of the 1800s, such as Aldin and Charlotte (Bailey) Grout in Africa, Edward Bailey in Hawaii, and DeBlance Scriber (grandfather) across the Iroquois Confederacy of Indians of central New York State. The great grandfather of DeBlance (Stephen Scriber) was actually captured and moved to Canada with his mother and two sisters during the 1780 massacre by the Indians led by Thayendangea (= Captain Joseph Bryant) near Fort Plank (see *The Bloodied Mohawk* by K. D. Johnson 2000). Luckily for Mark, Stephen was eventually released and returned to central New York at the demand of New York Governor Clinton after a year

did convince him that the ideal job would be to become a university professor to research and teach "natural history." This effort was catalyzed by undergraduate (1966–1970) and graduate (1971–1975) years at Cornell University in Ithaca, NY, and continued into a postdoctoral fellowship with the Rockefeller Foundation's "Conquest of Hunger" program (1975–1976) to work with plant breeders at Cornell and in Mexico to develop insect-resistant corn (maize).

After a brief flirtation as a bioscience major (for premed), Mark came to his senses after an inspiring entomology course sophomore year by Dr. George Eichwort and after a summer spent on the insect community ecology research with Dr. Richard Root (capturing cabbage plants and all of their insect community members). These experiences kept him on an entomology trajectory, but it was the first chemical ecology course taught in the USA that cemented Mark's research interests. This multi-lecturer course (with Wendell Roelofs, Tom Eisner, Martin Alexander, Robert Whittaker, etc.) was coordinated by a new young professor from Oxford University, Dr. Paul Feeny (Fig. 10.4). As an undergrad, Mark started a senior research project with Paul to determine whether cyanogenic and non-cyanogenic trefoil genotypes

Fig. 10.4 At Cornell University (Ithaca, NY), Mark developed a passion for swallowtail butterfly research and studied under the direction of Paul Feeny (major professor), John Franclemont, and Richard Root. Mark was also greatly influenced by Art Shapiro, Lincoln Brower, and Christer Wiklund. Linneaus not only named *Papilio glaucus* (from dark morph female in 1758, *Systema Nature,* Stockholm) and *P. turnus* (from a yellow morph female in 1771, actually of the same species) but he also papered his walls with colored book plates of *Papilio* butterflies in his summer home in Sweden

would differentially affect insect herbivores such as the southern armyworm *(Noctuidae)*. Eventually, a major theme for thesis research evolved around the assumption that the specialists would be more efficient at processing food for growth than generalists due to higher costs for polyphagous species (generalists) of maintaining and operating detoxification systems for the various and numerous different plant-based toxins (= "allelochemics").

Origins of Nutritional Ecology

Immediately upon commencing graduate research to experimentally determine feeding rates and efficiencies of caterpillars, a major problem emerged. The estimate of leaf biomass consumed could not be done on a fresh weight basis because leaves to be used in feeding containers continuously lost weight (and never stabilized in the reading) as they sat on the Mettler microanalytical balance. This frustration persisted for all species of excised plant leaves and required supplemental water via "aquapics" (such as used by florists to maintain turgor in their flowers). Estimated dry weight energy and biomass budgets could now be made, and the comparisons of assimilation and conversion efficiencies as well as consumption and larval growth rates could now be determined. The variable hourly leaf water database had a gap (due to the arrival of Mark and Kathy's first son, Brian) but was redone shortly afterward, with analysis of nitrogen and biomass efficiencies. The annoying importance of water in gravimetric analyses for insect feeding efficiencies (Scriber 1977) actually became a "science citation classic" for Current Contents.

To get answers to the question regarding differential efficiencies of being a specialist or generalist, it became necessary to examine many factors (in addition to leaf water) that might be involved in determining insect growth and food-processing "performance" and "costs" (metabolic, ecological, and evolutionary; see review, Scriber 2010). Several years of analyses of ecological energetics (caloric budgets) and plant nutritional value (the fundamental limiting influences of leaf water and nitrogen concentrations) with a fellow grad student (Frank Slansky, Jr.) revealed a basic pattern of herbivorous insect performance constraints and led to a major review of "nutritional ecology" of immature insects. Initially, their first draft of this review was 300 pages long with 1500 references! Despite the hopes of the authors, the editors of *Annual Review of Entomology* demanded a significant reduction in length. The resulting 30-page, 300-reference paper was published in 1981, but they felt this drastic reduction left only simply a skeleton outline of the more thorough job they had intended to do. The table of insect guild performance summaries was therefore published on microfiche later in *The Bulletin of the Entomological Society* in 1982, but this was still inadequate for most of the important information details. Therefore, it was expanded into a large review chapter (1985) at the request of editors for a 14-volume *Comprehensive Review of Physiology, Biochemistry, and Pharmacology.* Still not comprehensive enough, Frank expanded this into a book (with J. G. Rodriguez) of more than 1000 pages, with chapters for each "feeding guild" they had originally defined and examined! Nonetheless, the costs of generalization versus specialization remained elusive for 25 years (reviewed in Scriber 2010).

Other Tributes and Selection of Career-Long Research Organisms

Mark's swallowtail butterfly career track was basically shaped by a 1969 Cornell undergrad class assignment (term paper) describing the geographic range limits and the various biotic and abiotic factors constraining the current and historical distributions of selected species groups. He chose two species groups, the feeding generalist *P. glaucus* and the Lauraceae-specialized *P. troilus* sister groups. The academic pursuit of the constraints on species borders of these swallowtail species has continued long after that population biology class term paper assignment (of Peter Brussard). This research effort has in fact persisted as a focus of Mark's research for 45 more years.

Another term paper for a community ecology course (led by Robert Whittaker and Peter Marks) was actually initiated (as an undergrad) a year before Mark took the course. This effort involved documenting the geographical ranges (by latitude) and compilation by species of all recorded host plant records for the 570 species of Papilionidae of the world. This literature research quest was designed to help evaluate the prevailing ecological concept (assumption) that more species in the tropics would be specialized in their feeding ecology (narrower niches and greater "species packing") than at higher latitudes. Indeed, the results suggested that they were, and a general global pattern of latitudinal gradient in specialization was uncovered and published as Mark's first paper in 1973. Other Lepidoptera families have subsequently been evaluated by others and mixed results have been obtained (for discussion of several conceptual and biological problems testing this concept, see the review by Scriber 2010).

In the 2-year process of recording host plant affiliations for the Papilionidae from nearly 100 books in the archives of the Cornell Entomology Library, a potential graduate thesis topic arose: Are specialists more efficient than generalists at processing their food resources (do generalists on any particular plant species exhibit a higher metabolic cost for polyphagy than specialists) and the corollary (do specialists lose their ability to feed on ancestral hosts, i.e., burning their ecological and evolutionary bridges behind themselves after they specialize on particular hosts or phytochemicals)? These concepts were largely framed by current ecological theory, but the focus for experimental analyses became feasible and highly propelled by key references given to Mark by a graduate student teaching assistant, Arthur Shapiro. These classic papers were from Vincent Dethier (1954), Paul Ehrlich and Peter Raven (1964), and Lincoln Brower (1959). These papers reinforced the Papilionidae as a butterfly family well worth working with (and Dethier also suggested that the *Hyalophora* species group of Saturniidae or giant silk moths might be another).

Many of these species were collected and experimentally examined to determine physiological feeding efficiencies on various host plants using gravimetric techniques as the basis of Mark's 1975 PhD thesis research.

"Scriber's Folly" and the First Graduate School Crisis

With the generalist *P. glaucus* species group as the fundamental basis for comparisons of feeding efficiencies for various feeding specialists, Mark initially suffered from the inability to find or capture females. Hundreds of puddling males were easily captured in the Adirondack Mountains and in Tompkins County. However, only two or three females were captured during the first summer, and these would not oviposit on any plant species tested. Lack of eggs meant no larval feeding studies. Many experimental methods to stimulate oviposition (egg laying) were attempted until the construction of a large screen cage over one hillside on the Cornell University Campus. Small host trees were enclosed (natural and transplanted) and additional upper branches were allowed to be enclosed along the sides with meshing to seal them in. High-quality nectar sources were transplanted or potted flowers placed inside (at various heights). Roughly, 24 by 30 ft, the large cage was 18–20 ft high on the downhill side and had fiberglass screening on the top to roll back during the winters. This fiberglass screen destroyed Kathy's sewing machine but was only the first of many other sacrifices she has made to help her husband's career. Mark is greatly appreciative of her continuing patience, assistance, advice, and tolerance. This butterfly paradise quickly was dubbed by other grad students and entomology staff members as "Scriber's Folly" (Fig. 10.5). Cooperation of tiger swallowtail butterflies was moderate, but after about 10 more years, oviposition arenas on rotating platforms proved to be more efficient and rapid for individual female assays. Silk moths (Saturniidae) were also necessary to help distinguish between plant nutritional quality and degree of feeding specialization of the insects as causes for differential larval efficiencies and growth performances. While eggs were more easily obtained from field-captured moths (often laid inside paper bags), other problems with the use of moths soon surfaced for Mark personally.

In 1977, as a new assistant professor, Mark moved his young family to the west of Lake Michigan in the land of badgers, brewers, brats, beer, and bovines. As a field crop entomologist, the pest species of Lepidoptera he encountered in his research were boring (Hop-vine borers, Potato stem borers, and European corn borers). On the side, he quickly bootlegged some research with swallowtails and silk moths and obtained his first NSF Award. While his research led to some serious health issues (below), his recreational activities in the land of cheese and beer in Madison, led to a steady growth just above his beltline, which was affectionately dubbed a "Milwaukee tumor." This stuck as a nickname for two decades after leaving Wisconsin because his sons leaked it to the MSU Entomology softball team.

Fig. 10.5 Oviposition "cages" for *Papilio glaucus* females. "Scriber's Folly" in 1972 (with the top screen still rolled back from winter; on *upper right*) for multiple females later gave rise to round plastic multi-choice arenas for individual females *(bottom left)*. (Scriber 1993)

Severe Allergies to Lepidoptera Scales

After years of breathing airborne silk moth scales from frantic males trying to get out of their screen cages to "calling" females, Mark experienced repeated bouts of severe headaches and a weird neck and head chills shortly after entering the research lab with silk moth scales. Later, even the *Papilio* wing scales from many dozens of hand-pairings (and attempts) began to cause a similar reaction. After Mark's complaining about the headaches, his wife asked if he had been pairing butterflies that day. It was the "aha" moment and that led to the use of surgical masks for most future work. This also eliminated the need to switch insect taxa as a career choice, as was the case for other lepidopterists such as Chip Taylor.

At an International Conference on Lepidoptera banquet dinner in Cape Town, South Africa, in 1999, the main featured dish was of cooked silk moth larvae (the African mopane worms). Since they were cooked in a nice looking tomato sauce and since larvae lacked adult scales, Mark felt obligated to participate in the celebratory consumption of these Saturniidae and suffered no immediate physiological effects. However, shortly after, in the middle of the night he arose in a panic, unable to breathe. The old familiar headache and neck chills were accompanied this time with nausea and itchy throat with swelling which also made it difficult to breathe.

After an hour or two, the excitement subsided, and it was then decided there would be no future "worm eating" (due to possibility of more serious anaphylaxis).

Many different species of giant silk moths are eaten in Africa, and the price per pound for these delicacies is usually more than chicken, beef, or pork. A large series of postal stamps showing silk moths from different African nations attests to their importance. Mark inadvertently discovered the first written records (in 1840) of caterpillar consumption by humans in the letters from Charlotte Grout (the wife of missionary to the African Zulu people, Aldin Grout; see details in Scriber 2011b). A box of old letters (some with stamps, but most before paper postal stamps existed) given to Mark by his aunt Elizabeth (Scriber) Buscall proved to be a mini treasure chest of more than 70 missionary letters from and to Charlotte's family in the USA and Hawaii dating from 1838 to 1896. The Grouts returned to the USA in 1870 and died in Springfield, MA, in 1894 (Aldin) and 1896 (Charlotte), and it is feasible that they spent some of their final years at the nursing home of Isaac Buscall (the grandfather of Elizabeth's husband, Mark's uncle Frank). If so, this might explain how the letters Mark found may have come into the possession of Frank and Betty. These historically valuable letters were all recently transcribed by Mark and James Adams, and some excerpts have been extracted and published by Mole's Genealogy (http://molegenealogy.blogspot.com/2010/06/treasure-trove-of-american missionary.htlm).

It is interesting that Charlotte (Bailey) Grout had a brother (Edward Bailey) who also became an educational missionary sponsored by the American Board of Commissioners for Foreign Missions (ABCFM). He was sent to Honolulu in the Sandwich Islands (Hawaii) in April 1837 to teach the native people how to read (the Bible) and write in their own language and also share some of the moral values of New England Christian Yankees. Edward did much more in Maui than run the Wailuku Female Seminary and Mission (from 1841 to 1849). He was a famous artist, surveyor, naturalist/scientist, and businessman (founding a major sugar plantation; see Decker 2011). His Wailuku home was declared a Maui Historical Society Public Museum and it houses many of his paintings, parts of his valuable endemic snail collection, and much more. Mark recently made a trip to the Bailey House Museum to donate letters from Edward Bailey to his sister Charlotte from 1870 to 1896 and was enthusiastically received by the previous director of the museum, Linda McCullough Decker (Fig. 10.6). Many years of research for her book (Decker 2011) had only turned up two letters of Edward Bailey, so she was very grateful to have more.

A mystery was also solved for Mark at the Bailey House Museum regarding a drawing of *P. glaucus* and old entomological collecting equipment such as used by Edward for his classes (Decker 2011, p. 148). This drawing (see Fig. 10.6) traced back to a 1839 Lahainaluna engraving from the Bishop Museum entitled *Circular of the Sandwich Islands Institute with Directions for the Preparation of Objects of Natural History* (Honolulu, 1839 published by Pikao). They were adapted from Titian Peale's illustration and text (under the same title) from Philadelphia in 1831.

Fig. 10.6 The natural history teaching tools of Edward Bailey, an educational missionary during the 1840s in the "Sandwich Islands," now called Hawaii (Decker 2011). This 1839 drawing from the Bishop Museum was apparently redrawn from Peale's illustration at the Philadelphia Museum in 1831. The biographer of Edward Bailey (Linda McCullough Decker) and the current director of the Maui Historical Society's Bailey House Museum in Maui were pleased to receive the letters from Edward to his sister Charlotte Bailey Grout (1870–1896) which Mark donated. As with the incipient hybrid *Papilio* species (temporally isolated late-flight recombinants), so these missionary letters, too, were discovered in 1999 in the Battenkill River Valley area at the New York and Vermont border at his Aunt Betty and Uncle Frank Buscall's home

New England Origins (Native Americans, Missionary Zeal, and Speciation in Papilio)

The nineteenth century connections between three educational missionaries (Charlotte Bailey Grout with African Zulus, her brother Edward Bailey with native Hawaiian Maui, and DeBlance Scriber—Mark's grandfather—with several tribes of native North American "Indians" in central New York State, along the Mohawk River from Albany to Oswego) is currently the subject of research for a potential book that Mark is working on. The significance of central New York and Massachusetts (Mark's ancestry) in conjunction with the geographic origins and evolutionary dynamics of the eastern tiger swallowtail butterflies has been closely interwoven historically (Figs. 10.2 and 10.3).

In Holden, MA, Edward Bailey (born 1814) and Charlotte Bailey (later Grout; born 1811) grew up shortly after the Indian Wars following the American Revolution. One generation earlier, Stephen Scriber (a direct ancestor of DeBlance Scriber) was one of the few survivors of a famous massacre by Indians at Fort Plank (Fort Plane) on August 2, 1780, and he (at age 5 years, along with his mother and two sisters) was captured and taken to Canada by Indians for nearly 2 years before being released and returned to the area along the Mohawk River. His family continued to live along this river, and they witnessed the opening of the Erie Canal in 1815. Subsequent generations moved westward to central New York State. Meanwhile, halfway around the world, the ashes of the great Dutch East Indies (= Indonesian) volcano (Mount Tambora) erupted during April 5–15, 1815 and subsequently cooled the Earth's climate (mean of 0.7–1.3 ºF). 1816 was called the year without a summer, and there was snow and severe frosts in every month across New York and Massachusetts. Major food shortages across the northern hemisphere resulted from this atmospheric phenomenon in 1816, especially in the northeastern USA and Western Europe. Many in New England, near where Thoreau was born in the area in 1817, began to move west across New York State where they could reach the less rocky and more fertile soils of western New York and Ohio, and the Erie Canal made such dreams possible (Fig. 10.3). Among those moving west, into central New York near Lake Ontario, were generations of Stephen, Jacob, and Miner Scriber, followed by generations of DeBlance and Minch Scriber (Mark's father).

In North America, in addition to inspiring Mark, DeBlance Scriber taught "Indian" natives of the Mohawk, Oneida, and Onondaga tribes at various schools across central New York State from 1893 to 1924 during his younger years (Figs. 10.2 and 10.3). His dedication and self-sacrifice, and that of educational missionaries Charlotte Bailey Grout in Africa and Edward Bailey in Hawaii, was truly impressive. All of the missionary fervor generated in this New England region (New York State and Massachusetts) ran hand-in-hand with the transcendentalism movement, with a love of nature, belief in the individual, a passion for racial equality, and a complete commitment to service to others for the entire careers of these missionaries. As with H. D. Thoreau, R. W. Emerson, Thomas Merton, Aldo Leopold, and James Redfield, Mark's future career possibilities were mixing and fermenting with a focus that was more on the "spiritual" than "religious." He wondered what could be better than studying these symbols of a beautifully changing life-form metamorphosis and historically extensive earthly presence than the Lepidoptera (see *Hope for the Flowers* by Trina Paulus).

The Significance of Central New York State for Mark and Swallowtail Hybrids

Growing up in central New York State (Oneida, Hannibal, Oswego), many summers were spent near the Vermont border near Cambridge, NY (among covered bridges along the Battenkill River Valley). With Mark's undergrad, graduate, and postdoctoral programs completed in Ithaca and the Finger Lakes region, Mark's life was always geographically centered on what turned out to be an extensive hybrid zone between *P. glaucus* and *P. canadensis* (Fig. 10.3). This hybrid zone has now been identified as historically extending across most of New York State, and in this central region considerable taxonomic confusion existed for two centuries for many species (including various vertebrates as well as these tiger swallowtail butterflies) and later with the evolutionary divergence of ecotypes for the introduced European corn borer moths *(Ostrinia nubilalis)* as well as *Papilio*. The post-diapause spring emergences of temporally delayed recombinant hybrid populations at this juncture for univoltine and multivoltine Lepidoptera in New York State (across the Finger Lakes and the Mohawk River Valley into New England) has provided a mechanism of reproductive isolation and probable incipient hybrid speciation (via recombinant homoploids), which had generally been considered rare or impossible in animals. This area across central New York State, where Mark spent his grad school and postdoctoral research years with *Papilio* and corn borers, is precisely that which was occupied by Native American Indians for thousands of years (Fig. 10.3, and by the Iroquois League, or Confederacy, of five tribes since 1570) and later by European settlers, using the Erie Canal after 1815.

Later, Iroquois Indian tribe settlements in northern Michigan (where colorfully diverse and majestic red maples, white birches, and black spruce coexist peacefully) resulted in establishment of the Cross in the Woods National Shrine in the town of Indian River (dedicated to Kateri Tekakwitha, a young woman from Auriesville, NY). She spent her short life helping Native American smallpox victims along the Mohawk Valley from 1656 to 1680. This shrine (which has the largest crucifix in the world, made of a Pacific Coast redwood tree that was more than 2000 years old) is actually near Mark and Kathy's current lake home on Mullet Lake in northern Michigan. While these Indian natives occupied the postglacial Great Lakes region of Michigan and New York for many hundreds of years, the region of Northern Michigan (Lake Superior) was probably "mined" for copper long before by the global Minoan civilization (including China) in the Bronze Age, 2000 or 3000 years earlier (*The Lost Empire of Atlantis* by Gavin Menzies 2011). The Minoan Volcanic eruption of Thera in Greece (1650–1500 BC) destroyed much of this society and may have led to the story of "Atlantis"). Nonetheless, throughout this entire period of history, the swallowtail butterflies continued to reign strongly across the entire North American continent including the area we now know as the Great Lakes and New England regions as they had for millions of years before.

Million Years Ago: The Real "Native Americans" (the Pterourus Ancestral Clade of Tiger Swallowtail Butterflies)

Habitation of the Great Lakes region of North America by *P. glaucus* before and during Pleistocene glaciations southward to the Florida interglacial islands (Lehnert et al. 2012) may seem ancient. However, the occupation of the North American continent long before these glaciations consisted of an ancestral clade of swallowtail butterflies *(Pterourus)* that arose approximately during the Miocene, 24 million years ago, and likely occupied most of the North American plate (Condamine et al. 2013). These *Papilio* ancestors persisted and eventually gave rise to three current species in the eastern part of the continent, including what may have been a long-time hybrid zone between *P. glaucus* and *P. canadensis* across the Great Lakes region into what are now New York and Massachusetts and southward along the Appalachian Mountains. Evolving more recently (less than 100,000 years ago; Kunte et al. 2011) has been the hybrid "mountain swallowtail" species, *P. appalachiensis* (Ording et al. 2010; Scriber 2014). Studies and descriptions of these three species over the past four decades have been pursued and documented by Mark's research (see below).

Historical Post-Pleistocene Glacial Background for *P. glaucus* in North America

Strikingly prominent on the wing, relatively large North American tiger swallowtail butterflies have attracted attention for many centuries (including ancient cultures of Mexico; Tyler et al. 1994). The first picture known of an American butterfly was *Pterourus* (= *Papilio*) *glaucus* in a watercolor painted around 1587 by John White in "Virginia" (actually Roanoke Island, NC; Tyler et al. 1994; Pavulaan and Wright 2002), purportedly after a Native American boy had given him a specimen (the Native American name for butterfly was "manankanois"). This watercolor was reproduced in a woodcut by Thomas Moffet of London in 1634 (Fig. 10.7) and copied subsequently by several others from 1666 to 1699 (Pavulaan and Wright 2002). The tiger swallowtail is currently the state insect of Virginia and is featured on their automobile license plates (Fig. 10.8).

Artist-naturalist John Abbot in Georgia (between 1776 and 1840) finished 103 drawings of insects (of Georgia) for Englishman William Swainson during the years 1816–1818 (Calhoun 2007). The drawings had an extensive history up to their rediscovery in 1977 in the library of Alexander Turnbull in Wellington, New Zealand. Swainson moved from England to New Zealand in 1840. According to the historical account assembled by Calhoun (2007), a large portion of his library was auctioned in June 1840, but in 1841, a ship carrying much of the remaining items of the library sunk off the coast of South Africa (incidentally at the very time the Grouts were settling into Umvoti to start their mission with the Zulu). Until 1977, the drawings of Abbot were assumed to be lost, but a librarian at the Alexander Turnbull Library in New Zealand rediscovered them. The drawings of Abbot were partially based on duplicate illustrations as was the case for many artists, including Mark Catesby, who in 1736 replicated (and perhaps traced) the drawing of John White. Catesby acknowledged that his 1725 drawing of the South Carolina tiger swallowtail butterfly was based on White, which was common at the time (see www.Smithsonianmag.com/arts-culture/Mark-Catesbys-New-World.html).

The classic *Natural History of the Rarer Lepidopterous Insects of Georgia* (Smith and Abbot 1797) was the first major treatise on North American insects, and it used reproductions of the drawings (during 1776–1792) of John Abbot. Currently, 80 copies of the 1797 book are known in six countries. A continuation of the book

Fig. 10.7 Early attention to *Papilio glaucus* was evident as the first butterfly figured in North America (by John White in 1587 of Sir Walter Raleigh's third expedition to Virginia/North Carolina). This drawing (not shown) led to a woodcut reproduction by Thomas Moffett in 1634 and was later duplicated by Mark Catesby in 1725 *(at top)*. Subsequently, Linneaus described specimens sent in 1748–1751 (see text). The beautiful paintings of John Abbot (1816–1818) included both yellow and dark morph females of *P. glaucus,* intended for expansion of his rare book, *Insects of Georgia* (1797). Henry David Thoreau also described local tiger swallowtails at Walden Pond (near Boston) in both 1859 and 1860, although based on the historical thermal constraints (see Fig. 10.3), it is most likely that these were *P. canadensis* rather than *P. glaucus*

with drawings by Abbot (1816–1818) of insects that were not figured in the 1797 *Insects of Georgia* was the one commenced for W. Swainson, who decided not to publish this continuation due to increased costs of production (Calhoun 2007), however, in honor of the 250th anniversary of Georgia's founding as a colony (in 1733). The Alexander Trumble Library issued the first installment of its unique set of 103 watercolors by John Abbot commissioned by Swainson. The library had acquired them in 1927. It is interesting that the first butterfly template completed by Abbot (during the 1816–1818 paintings) was of the dark morph female of *P. glaucus,* and, later, the yellow morph female of *P. glaucus* was featured with its larvae on *Ptelea trifoliata* (hop tree of the Rutaceae; Fig. 10.7). This and other insects were likely to be from Burke County, GA, where Abbot lived for many years before 1806 when he moved to Savannah (Calhoun 2007). The reproduced paintings of the first set of six insects (J. Abbot, Fascicle One, 1983; publ. Turnball Library, New Zealand) were found by Mark Scriber in an antique shop near Athens, GA, in 1997. It included larvae, pupae, and an adult of *P. glaucus* on a hop tree (Fig. 10.7).

New England and the Origins of the Mountain Swallowtail "Hybrid Species"

In early June of 1859 and 1860, Henry David Thoreau also described *Papilio* tiger swallowtails in Massachusetts near his rivers and streams (2013; butterfliesofmassachusetts.net/east-tiger-swt.htm). It turns out that the state of Massachusetts (except the coastal area in the southeast; Fig. 10.3) represents what appears to be a large hybrid zone, an extension from the Great Lakes and New York State. Much of the state has shown the mid-July ("false-second"-generation) late-flight morphology and are probably recombinant hybrids with mixed diagnostic traits from both of the parental *P. glaucus* and *P. canadensis,* as seen in the late flight at the New York/Vermont border in the Battenkill River area (Scriber 2011a). Such areas with hybrid late flights are inside the thermally defined hybrid zone where 2300–2700 degree days (above base 50 ºF) occur, and these areas do not permit a second generation to be successfully completed (see Fig. 10.3). Dark morph females (apparent mimics of *Battus philenor*) have not been recorded in Massachusetts and have historically reached their northern limits just to the south. Recent climate warming since 2010 (with many areas exceeding 2800 degree days) has created a new thermal landscape where bivoltinism (2 generations/year) and dark morph introgression from *P. glaucus* are certainly now possible across much of Massachusetts (Scriber et al. 2014). It is unclear whether Thoreau had witnessed the *P. canadensis* or *P. glaucus* species.

All three tiger swallowtail species in eastern North America (*P. glaucus, P. canadensis,* and *P. appalachiensis*) were considered together as the "eastern tiger swallowtail" after a dark morph female description by Linnaeus in 1758 from a specimen obtained from Peter Kalm during his travels in mid-Atlantic states during 1748–1751. Later, in 1771, Linnaeus described *P. turnus* from a yellow morph female of *P. glaucus*. The Canadian swallowtail was described as a subspecies of *P. glaucus* in 1906 by Rothschild and Jordan and elevated to species status by Mark's research group (Hagen et al. 1991). It was interesting that the Canadian government had already implied that this status was deserved when they unveiled the first day issue postage stamp of the "Canadian swallowtail" at the 1988 International Congress of Entomology in 1988 at Vancouver (see Figs. 10.8 and 10.9). As seen with kings, queens, and presidents, the Canadian swallowtail was also honored on a special issue of a 50-cent coin in 2004, and in 2013, the Royal Canadian Mint also produced a pure silver $20.00 coin with a large, beautiful, full-colored, *P. canadensis* image (Fig. 10.9). Perhaps someday this cryptic *P. appalachiensis* species will be honored with a US coin or stamp as one of the very first animal hybrid species ever to be described. The eastern tiger swallowtail, *P. glaucus,* is celebrated as the state insect (or butterfly) in six states (Alabama, Delaware, Georgia, North Carolina, South Carolina, and Virginia) and other states have five additional *Papilio* species so designated.

Fig. 10.8 The *Papilio glaucus* species has not been recognized on any coins to date, but the image appears on many different postal stamps from several continents and at least 32 different countries (e.g., on a 2012 stamp from Kosovo; *bottom right*). In the USA, six states have the eastern tiger swallowtail as the official state insect (or butterfly), including Virginia, which has it prominently displayed on its license plates. The official postal first day issues for *P. glaucus* (1987) and for *P. canadensis* (1988) are shown at the *top*

Fig. 10.9 The "Canadian tiger swallowtail" has been celebrated in Canada by the issue of a stamp in 1988, and a 50-cent coin in 2004 with the prominent image of the butterfly. An even more impressive tribute to this species was issued by the Royal Canadian Mint as a large 20-dollar sterling silver coin in 2013 with a scientifically accurate color image

Collecting Stamps with Papilionidae Images

The urge to collect specimens and compile a complete set of all 570 species of Papilionidae was suppressed by Mark's conversion to collecting stamps of insects instead. The restraints with threatened and endangered species had escalated to where this would have been impossible in any case. The influence of May Berenbaum and Charles Covell was immense for Mark's shift in focus from pinning to philately. The *P. glaucus* and *P. troilus* species groups have been favorites from the beginning of Mark's Lepidoptera career. Others around the world also seem to enjoy the image of *P. glaucus* since they are on at least 37 different postal stamps from 32 different countries (e.g., Syria, Eritrea, Tanzania, Angola, Liberia, Ghana, Congo, Central Africa, Malaysia, China (Taiwan), Cambodia, Kosovo (Fig. 10.8), Guyana, Nevis, Grenada, Nicaragua, as well as the USA and Canada).

Stamp Collecting and a Brazilian Discovery (at Keith Brown's Home)

Mark's first sabbatical leave in 1998–1999 included a visit (2 months) to Brazil where he taught a course on invertebrate conservation at the University in Porto Alegre for Helena Romanowski. One class field trip was a half-day drive into the beautiful, panther-filled forests near the Argentina border, but this was a physical challenge for Mark. With failing hips causing uncomfortable visions of the end of his field-career, Mark struggled to keep up with Helena and Ana Morais as they led the fast-paced hikes through the slippery slopes and forest hillsides, across small canyons on slippery giant fallen log "bridges." It was not only his exhaustion that was a problem, it was the pain in his hips and weakness of a single leg that required him to crawl across these logs, repeatedly falling further behind the group. Upon return to Michigan, both hips were replaced within the year (2000), and a new millennium of fieldwork could commence!

The next Brazilian experience was Mark's return to Campinas to stay with Keith Brown at his home near the University of Campinas. Mark brought back some Brazilian stamps (among others found at stamp shops in Porto Alegre). Upon showing four of these (1979 issued; Scott # 1621–1624; Fig. 10.10) to Keith, he said that two of them actually looked a lot like some slides he had taken years ago. He retrieved the slides, and to our amazement, the stamps looked exactly like Keith's slides. In fact the images on both stamps even had the edge of a leaf and identical shadows (as did the third and fourth stamps) that were in Keith's slides! All of Keith's four stamps had been published in a Japanese book (*Brazilian Insects and Their Surroundings* published by Koyo Shoin Co. Ltd.) by a postdoc (L. S. Otero) that Keith had once lent his slides to. It was apparently these four images that the Brazilian artist copied to produce the postage stamps issued. Furthermore, these published butterfly or stamp images were subsequently copied for the special first day cover issues (August 1, 1979) used for the "Flora and Fauna of the World" project (Fig. 10.10).

Fig. 10.10 Unknown to him, all four Brazilian postal stamps from these 1979 issues were derived from slides that Keith Brown had himself taken (see text). Even the shadows of the butterfly and a plant leaf in Keith's original slide photo were reproduced by the Japanese book, and later painted for the stamp, and reproduced again in the color plate on the envelope

Mark's days with Keith Brown in the BioPreserve near Campinas were truly an enriching and mind-expanding experience. The entire day in the humid jungle-like trees consisted of nonstop collecting, releasing, and observing butterflies. The daily allocation Keith selected was consistently one canteen of water and half a package of Oreo cookies for each of them. The various trails, transects, and traplines were faithfully examined daily for butterfly species and numbers as they had been for years. In addition to natural puddles, the baits included poop, pee, and pulverized fruits, all of which we also needed to restock daily. They returned to Keith's home in the evening after the standard university supper and watched bats flying through his open-air living room as they discussed philosophy and spirituality (his wife, Kay, had just died a couple of months earlier). Also over the course of a few days, we watched a continuing invasion of thousands of large ants marching through the house. At night Mark gazed at dozens of geckos on the ceiling and wondered if they were eating these ants or if they were eating the local screwworm flies that had infected one of Keith's wounded dogs. Shortly, the geckos began to decline and Mark wondered if these had fallen prey (as Keith had seen previously) to the giant lycosid hunting spiders (that were, with legs, roughly 3 in. in diameter and actually audible in their running around his bedroom at night). Mark kept his toes tucked under the sheets at night even though both the heat and humidity were very high.

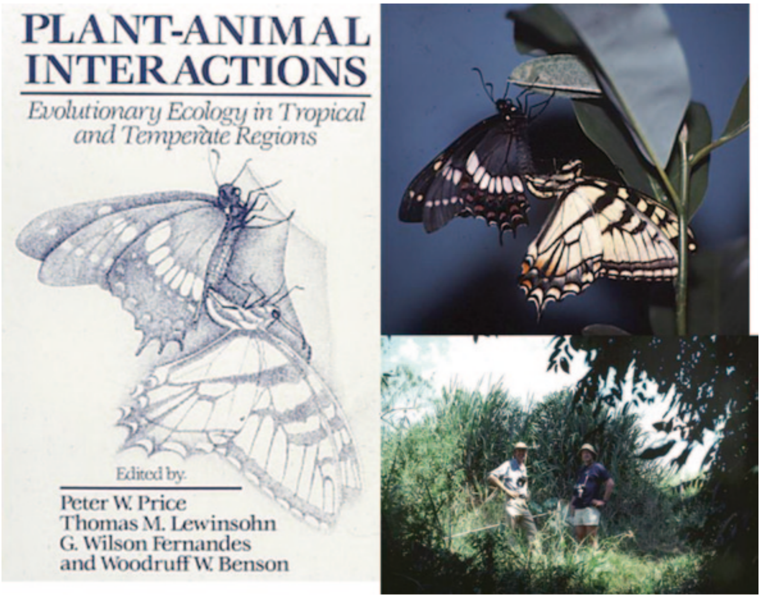


Fig. 10.11 The interspecific (and intergeneric) hand-pairing of the Brazilian *Papilio* (= Pyrrhosticta; part V) scamander female with a *Papilio* (= Pterourus; part III) *glaucus* male in the Scriber lab made the cover of a 1991 Wiley book (edited by Peter Price, Thomas Lewinsohn, Wilson Fernandes, and Woody Benson) on evolutionary ecology in tropical and temperate regions. Keith Brown and Paul Feeny are shown at the collecting site near Campinas

One day Mark watched Keith draw drinking water for the canteens and asked what the water source was. Keith said it was from a shallow hand-dug well under the house, which itself was surrounded by foot-deep floodwater from the adjacent animal farm hillside. He asked whether it was really safe to drink, and Keith explained that it was chemically treated in the large glass container filled with scary-looking greenish, reddish, and bluish coated spiral glass tubes. Since Keith was still alive, Mark decided to drink this water rather than dehydrating and facing likely kidney stone attacks as once before in Mexico (on a 2-week collecting trip with Skip Nault and Tom Wood). There was also the concern that Brazil might also create the affliction Mark experienced in Mexico, sometimes called Montezuma's revenge, the Aztec two-step, or the "Mexican seeping slickness."

In the end, Mark survived and had a very successful trip to Brazil, and he was able to witness a true Lepidoptera legend in action! Keith Brown was an absolutely amazing naturalist, knowing essentially everything in the area as well as changes in their populations. Mark has never in his career seen anyone else able to this, although Keith's student Andre Frietas came close. With US Department of Agriculture (USDA) permits, Mark had secured specimens of the most generalized *Papilio* species in Brazil *(P. scamander)* as well as some other species to bring back to Michigan for hand-pairings (and bioassays) with *P. glaucus* and *P. troilus*. One such previous hand-pairing (*P. glaucus* with its distant relative, *P. scamander*) was featured on the book cover of the Brazilian Conference on Herbivores (Fig. 10.11).

An Australian "Cryptic Species" and Reevaluation of Latitudinal Gradients in Feeding Specialization for the Papilionidae in the Tasmanian Wilderness

Determination of macrogeographic (and local) patterns in feeding specialization in herbivorous insects such as the Papilionidae requires appreciation of numerous biotic and abiotic factors (Scriber 2010). However, biodiversity is dynamic in nature and generally is a result of genetic diversity, not just species diversity (Scriber 2014). Subspecies have been important, but additional attention to "cryptic biodiversity" (genotypes) will be needed in the face of rapid environmental changes such as climate (Balint et al. 2011). To assess the degree of ecological and evolutionary specialization in one of the most polyphagous species of swallowtails worldwide, Mark went to the Australian *Graphium macleayanus macleayanus* subspecies, which has been reported on at least five different families of host plants across its broad geographic range from tropics (15′S latitude) to Tasmania (42–43′S latitude). In contrast, its *G. macleayanus moggana* subspecies occurs only where its single host plant species (southern sassafras, *Antherosperma moshatum*) occurs in Tasmania and southernmost Victoria, Australia.

Mark's attempts to capture and rear the *G. m. moggana* subspecies (Scriber et al. 2008) were in many ways more challenging than getting eggs from *P. g. glaucus* or *P. g. canadensis* during his thesis years. With the assistance of Geoff Allen and Peter McQuillan, Mark was able to capture hilltopping males on the side of Mount Wellington near Hobart, Tasmania, but never saw a female. The next week Peter and his 11-year-old son took Mark up into the Mount Field international biome wilderness, where they were able to capture a few females by leaning over the mountainside and using very long nets to reach the treetops. Unfortunately, the success in getting oviposition from all of these females was zero, despite using every trick known to induce egg-laying by female butterflies (e.g., walking them gently across host leaves, using lights in front of oviposition arenas, and sleeving them on their host branches). Realizing this seemed hopeless, Mark had to resort to field-collecting young larvae on the trees themselves by spotting notched feeding on leaves in the canopy. Help from Geoff, Peter, and their associates at the University of Tasmania insured some success (Scriber et al. 2008).

Before leaving Mount Field wilderness where another egg-laying herbivore, the duckbilled Platypus, swims in mountain lakes, Peter McQuillan took Mark to a special spot above the treeline to see some geometrid moths that he worked on (310 species in Tasmania). Although very cold and rather windy, Mark spotted a small very attractive moth fly out from the low-lying shrubs and land on a rock in the sunlight on the path. Precisely at the time Peter exclaimed that this was a new species of Geometridae that he had not seen before, his overly enthusiastic young son came sweeping in for a running net shot to capture it. However, instead of fame he had hoped for, he smeared the specimen across the rock! Mark is virtually certain that this incident may represent the shortest duration on record from recognition and discovery of a new species to its local "extinction" (about 1.5 s).

The Mount Field wilderness was an especially productive site for collecting larvae of *G. m. moggana* on young southern sassafras trees. Set in a beautiful and unique prehistoric-looking land of large tree ferns and eucalyptus trees, the sassafras *(Atherosperma moschatum)* thrived in moist areas. Within 15 min Mark had collected several larvae and came back to share his excitement. That is when Geoff asked if Mark had checked his body for land leeches, which were known to be very abundant in this area. Quickly the two professors dropped their trousers and began picking off several large, very fast-moving leeches (which actually looked as if they were "running" up their legs). Paul Walker, a postdoc with Geoff Allen, was not comfortable getting help picking leeches and he did his own. However, an hour or two later, we reached the university and parked the truck. When Paul got out, he had the entire back of his jeans soaking in blood behind his knee. This was most likely caused by the ball of blood (a leech, more than an inch in diameter) found rolling around in the dirt on the floor in the truck.

Many strange and beautiful animals were seen in Australia (Tasmanian devils, kangaroos, wallabies, rainbow lorikeets, etc.). However, one of the strangest encountered by Mark (and his wife, Kathy) was seen in a small town in the mountains east of Canberra. Upon returning to their car after some local shopping and tourism, Mark was startled by a huge round, brown, hairy face that filled the passenger window of the car parked directly next to them, with its large claws hanging over the lower window frame. After a brief startled recovery period from brushing against this thing, Mark noticed that there was a driver inside with this animal. He then explained that it was his pet wombat whose Mom was killed by a car. He raised this wombat from a tiny baby and for many years had taken it into town every Sunday to get an ice-cream cone. Apparently, it had just finished the cone before shocking Mark.

More Field Collecting Disasters Having scheduled a 3-day layover in Oregon and Washington, after an entomology conference in Asia, Mark hoped to collect (for his first time) the northwestern members of the *P. glaucus* species group *(P. rutulus, P. eurymedon,* and *P. multicaudatus)* to bring back to the lab for bioassays and matings. After using the wooden net handle and carefully climbing through rather widely spaced big electrified wires, Mark was successful at capturing a few nectaring *Papilio* along this powerline cut on the hillside. However, the excitement of this success, the heavy sweat that soaked his clothes, and the ease with which he got through these electric wires earlier, all combined to give him the hardest jolt across his back and body he had experienced since high school football.

A couple miles later, along a steep hillside, he spotted two large females of *P. rutulus* that were nectaring on 5–6 ft tall flowers on the edge of the road. Again, so excited to see these in the field and to actually have a shot of catching them, Mark quickly stretched out and got both specimens in the net at the same time. However, the steepness of this hillside was hidden by the height of the flowers and with the momentum of the swing, he free-fell about 8 ft, crashing to the bottom of some flowers and continued rolling down the very steep hillside, flipping four or five times, mowing down a sizable patch of vegetation. Smugly (proudly) twisting the net during these rolls prevented loss of the butterflies, and after taking account of minor injuries, he quickly ascended the steep hillside and drove on to find a motel for the night. In order to keep these highly prized live butterflies preserved until getting back to the lab in Wisconsin, he put them in their ziplock plastic (to prevent ice from getting them wet in the field cooler) and put them in the motel refrigerator for the evening. After getting new ice for the cooler the next day, he pulled out the bag of hard-earned specimens and realized they were all frozen solid! The refrigerator freezer combination was set too cold and the entire unit acted as a freezer, killing every one of the specimens from the previous 2 days.

International Ecology Meeting in Japan: Origin of the Swallowtail Butterfly Book

Some of the language hurdles in butterfly biology and ecology research were reduced by joining the Japanese for a symposium and cultural exchange that resulted in a book (Fig. 10.12; Scriber et al. 1995). Among the most prominent authors was geneticist Sir Cyril Clarke (1907–2000). A few years earlier, Mark asked Cyril for a complete set of his reprints in 1984 and was totally amazed when he very soon received a box in the mail that weighed nearly 40 pounds with hundreds of beautiful publications (many in color) and a note from Cyril: "I assumed that you did not want my medical publication reprints." He subsequently wrote a chapter for the swallowtail butterfly book, and after 3 years of deception and delay by Cornell

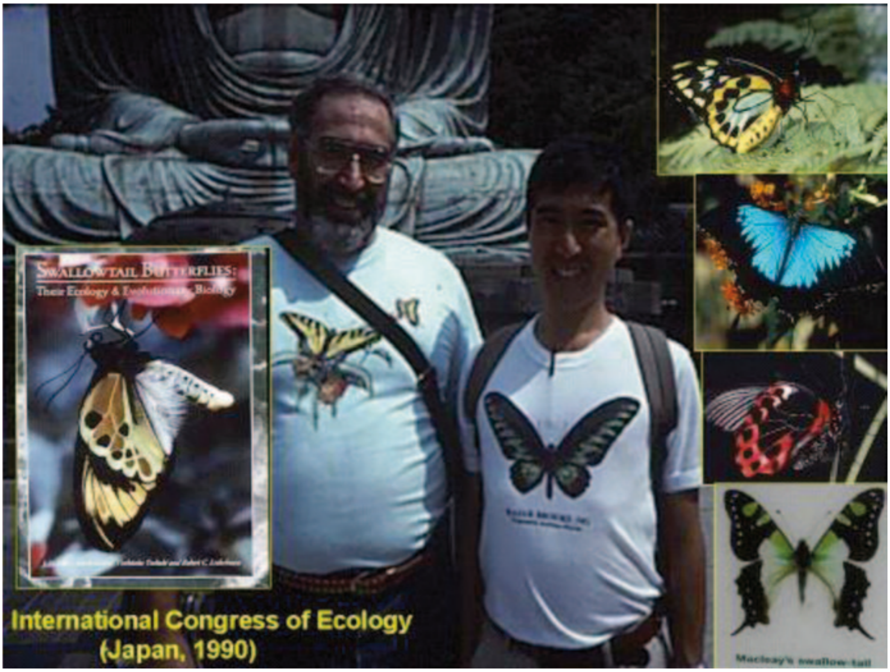


Fig. 10.12 *Swallowtail Butterflies: Their Ecology and Evolutionary Biology* was a book (1995, Scientific Publ., Gainesville) that resulted from a symposium at the 1990 International Congress of Ecology in Japan. Mark is shown with Ritsuo Nishida (both in their favorite T-shirts)

University Press, Scientific Publishers finished the book off very quickly for publication. Nevertheless, because of these delays since 1990, in 1994, Cyril wrote Mark and expressed his concerns about the delays since 1990 and said, “I do look forward to its publication,…hopefully before I am under the sod.” Cyril’s research on nonrecombining genes (supergene) regulation of mimicry was done 50 years before modern molecular genomics confirmed much of his work (e.g., with the possibility that the different linked genes were perhaps different mutations of the same gene; Kunte et al. 2014).

From Biological Forests to the Political Jungle: Criticism of “Congressional Pork” and Subsequent Scientific Consequences

As the introduced gypsy moth devastations spread through the Midwest and the Appalachian Mountains in the late 1980s, a major chunk of federal money ($5 million) was announced for proposals solicited to research the “nontarget” impacts of gypsy moth management programs. Mark coordinated and wrote a multi-investigator proposal from the State of Michigan despite discouraging (and even alarming) statements from USDA Forest Service personnel that it was a waste of effort because everyone knew this was simply a thinly veiled scientific sham and that all the money was planned to go to West Virginia (Senator Robert Byrd’s state). Nonetheless, the Michigan team submitted a very strong proposal that built on strong local scientific expertise and the impact of pesticides (even the Lepidopteran-specific *Bacillus thuringiensis* var. *kurstaki* (Btk) types) on the endangered Kirtland’s warbler and the threatened Karner blue and Mitchell’s satyr butterflies. After meeting the announced deadline, Mark was subsequently told that the MSU proposal received almost every first place ballot from the review committee; however, it was somehow decided that these proposals were now considered only preliminary and that full proposals would now be sought, and, furthermore, they should be focused on mountain range transects and amphibians that reach high diversity such as seen in the Appalachian Mountains. Clearly, this was an attempt to eliminate Michigan from contention.

This slightly modified Michigan’s proposal again received strong support in the scientific review process (apparently it could not easily be tossed out), but it was decided that the money should best be split $2.5 million each between Michigan and West Virginia. Unfortunately, just before funds were released for this research, Congressman Robert Traxler (appropriations committee chair) took his campaign chest funds and retired to shortly later become a trustee at MSU (in 1993). With a sudden vacuum in political clout in Washington to counter Byrd and others, the money flow was all quickly channeled to West Virginia (to get more preliminary data) and then in subsequent years to follow up on the pilot data (just as the forest service friends had told Mark it would happen).

In Michigan, at about the same time, calls from several West Coast and Midwest radio stations and other colleagues were asking if it was the Michigan State Scriber lab proposal ("sex lives of butterflies" according to several radio stations and newspapers, including Mike Royko's column in Chicago) that was being rescinded by Congress for unneeded and wasteful spending of government funds. It turned out that there was a shake-up at the NSF when Congress decided to rescind funding for 31 proposals (including one at MSU led by Bob Lederhouse and Mark Scriber).

Apparently, the US Congress was getting very tired of criticism from "basic" scientists for its lack of peer review and silly-sounding "pork research" as in various commodity grants for particular crops or pests for their own states (for which Senator Byrd was quite a leader). In 1992, Congress decided not politely, as a "tit-for-tat" type response, that in the future, all National Institutes of Health (NIH) and NSF funding would cease until young congressional "aides" could review every proposal before allowing any official funding from NSF. Such a nightmare for the future of NSF and NIH and the entire scientific community was averted in a compromise; NSF gave up $2 million in their budget, originally to rescind 31 grants that had been threatened. However, these grants had already expired with their funds already spent; so the scientific community did not get upset. NSF apparently "ate" these cuts elsewhere in their budget.

The *Chronicle of Higher Education* (July 28, 1992 issue) interviewed Bob Lederhouse (Mark's Co-Principal Investigator, Co-PI) and discussed this dangerous congressional behavior. As a result, the NSF now requires careful justification for each proposal and may include basic scientific training of students and postdocs, provision of data for public use (e.g., Genebank), workshops and training of high school students, expansion of public science education (including things such as programs at butterfly houses and insect zoos), and international collaborations. Justification of the Lederhouse/Scriber research could also have been easily presented if the implications of mate selection for population regulation of pest species could have been highlighted. However, the proposal would in that case most likely have been sent from NSF (whose mission was clearly basic research) to the USDA Competitive "Biostress on Plants" Grants Program (which focused more on applied research and for which Mark had previously served as a panelist and also as program manager). Both federal research agencies were always trying to reduce duplicate proposals (that were basically identical to both agencies) to be efficient with their resources!

Even without forest service or federal gypsy moth nontarget impact funding for their research, Mark and his students were nonetheless able to determine that, even with the relatively safe Btk insecticidal sprays, the nontarget impacts were devastating for Lepidoptera, including *Papilio,* at least for 4–5 weeks post spray, despite being in the direct sunlight and exposure to rain. As a result of misleading statements by some of the chemical manufacturers about some serious nontarget impacts of insecticidal gypsy moth sprays, skepticism was also at a peak a year or two later when genetically engineered corn plant pollen was found to kill monarch butterflies. Economical and political scuffling occurred for a couple years between environmentally concerned scientists and the producers of these genetically altered corn plants. However, it turned out that the maize pollen didn't travel very far in the wind (unlike pine pollen for example). Also, the timing of pollen production and monarch movement/feeding did not overlap as extensively as thought, and the risk to nontargets was not as acute or severe as feared (Scriber 2001). It seems that herbicides are a bigger threat to milkweeds and monarchs than the insecticidal corn tissue and pollen (monarchjointventure.org/threats/breeding-habitat-loss/).

Conclusions

A career overview (for JMS) has shown that a continuous integration and synthesis of natural history analyses and experimental probings (with controls) have revealed *processes* as well as *patterns* in insect–plant interactions. Considerable efforts were spent defining and examining specialists and generalists (by plant taxon or chemotypes) and also identifying and differentiating host races, subspecies, cryptic species, and hybrid species (Scriber 2011a). Subsequent analyses of "species borders" revealed extensive geographical and genetic introgression. Mark's major academic conclusions are that neither "host specialization" nor "interspecific hybrids" are evolutionary "dead ends" but rather may serve as a very important part of the processes enhancing biodiversity (Scriber 2010). Public science education efforts (e.g., butterfly houses and insect zoos; Fig. 10.13) and citizen scientist involvement in large programs such as Monarch Watch provide a strong support base for future

Fig. 10.13 Public science education programs using butterflies have become internationally extensive, with at least 350 permanent butterfly houses or insect zoos. The International Consortium of Butterfly Exhibitors and Suppliers (ICBES) has met at many locations, including some featuring exciting and fascinating nature expeditions described by Mark (see text)

Fig. 10.14 Reflections of collections (Australia, Costa Rica, Alabama) and recollections in retirement "takes the cake"

research and funding justification beyond pure science. It has become more and more evident that social, political, and religious forces shape biodiversity conservation and resource sustainability at local, regional, and global levels (Scriber 2014).

An appropriate summary comment regarding life lessons from Lepidoptera has been offered earlier by two New England transcendentalists: Nathaniel Hawthorne (1804–1864) who said "Happiness is as a butterfly which, when pursued, is always beyond our grasp, but if you will sit down quietly, may alight upon you"; and by Henry D. Thoreau (1817–1862) who similarly said "Happiness is like a butterfly. The more you chase it the more it eludes you. But if you turn your attention to other things, it comes and sits softly on your shoulder." The preferred scientific approach of using "strong inference" over "eternal surveyor" was expounded by many mentors since the paper by Platt (1964, Science, 146: 347–353). However, during his career, Mark found that, instead of experimentally forcing the scientific questions, he could let the butterflies naturally lead him to the ecological/evolutionary answers. As he relaxed, observed, listened, and surveyed biological variation (geographically) over the decades, the fundamentals of insect nutritional ecology, hybrid zone dynamics, and some secrets of animal "hybrid speciation" were uncovered (or "emerged") from these butterflies and "alighted," somewhat unexpectedly, on Mark's academic shoulders. The deep personal satisfaction of these discoveries at the end of a career are equally great as the initial enthusiasm generated and wonder provided by "natural landscapes and processes" at the beginning (Fig. 10.14). Thoreau also said, "None are so old as those who have outlived enthusiasm."

References

Bálint M, Domisch S, Engelhardt CHM, Haase P, Lehrian S, Sauer J, Thessinger K, Pauls SU, Nowak C (2011) Cryptic biodiversity loss linked to global climate change. Nat Clim Change 1(6):313–318. doi:10.1038/NCLIMATE1191

Calhoun JV (2007) John Abbott's butterfly drawings for William Swainson, including general comments about Abbot's artistic methods and written observations. J Lepid Soc 61:1–20

Condamine FL, Sperling FAH, Kergoat GJ (2013) Global biogeographical pattern of swallowtail diversification demonstrates alternative colonization routes in the Northern and Southern hemispheres. J Biogeogr 40:9–23

Decker LM 2011. Edward Bailey of Maui: teacher, naturalist, engineer, and artist, 1st edn. Rainsong, China, p 352

Hagen RH, Lederhouse RC, Bossart JL, Scriber JM (1991) *Papilio canadensis and P. glaucus* (Papilionidae) are distinct species. J Lepid Soc 45:245–258

Johnson KD (2000) The Bloodied Mohawk: the American revolution in the words of Fort Plank's defenders and other Mohawk Valley Partisans. Picton Press, Rockport, p 752

Kunte K, Shea C, Aardema ML, Scriber JM, Junger TE, Gilbert LE, Kronforst MR (2011) Sex chromosome mosaicism and hybrid speciation among tiger swallowtail butterflies. PLoS Genet 7(9):e1002274. doi:10.1371/journal.pgen.1002274

Kunte K, Zhang W, Tenger-Trolander A, Palmer DH, Martin A, Reed RD, Mullen SP, Kronforst MR (2014) Doublesex is a mimicry supergene. Nature 507:229–232. http://dx.doi.org/10.1038/nature13112. Accessed 13 March 2014

Lehnert MS, Scriber JM, Gerard PD, Emmel TC (2012) The "converse of Bergmann's rule" in tiger swallowtail butterflies; boundaries of species and subspecies wing traits are independent of thermal and host-plant induction. Am Entomol 58(3):156–165

Menzies G (2011) The lost empire of Atlantis: history's greatest mystery revealed. Harper Collins, NY, p 374

Ording GJ, Mercader RJ, Aardema ML, Scriber JM (2010) Allochronic isolation and incipient hybrid speciation in tiger swallowtail butterflies. Oecologia 162:523–531

Pavulaan H, Wright DM (2002) *Pterourus appalachiensis* (Papilionidae: Papilioninae), a new swallowtail butterfly from the Appalachian region of the United States. Taxon Rep 3:1–20

Rothschild W, Jordan K (1906) A revision of the American papilios. Novitates Zool. 13:411–744

Scriber JM (1977) Limiting effects of low leaf-water content on the nitrogen utilization. Energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). Oecologia 28:269–287

Scriber JM (1993) Absence of behavioral induction in oviposition preference of *Papilio glaucus* (Lepidoptera: Papilionidae). Great Lakes Entomol 26:81–95

Scriber JM (2001) Bt or not Bt; Is that the question? (Invited Commentary on 6 Bt corn pollen articles) Proc Natl Acad Sci U S A 98:12328–12330

Scriber JM (2010) Integrating ancient patterns and current dynamics of insect–plant interactions: taxonomic and geographic variation in herbivore specialization. Insect Sci 17:471–507

Scriber JM (2011a) Impacts of climate warming on hybrid zone movement; geographically diffuse and biologically porous "species borders". Insect Science 18:121–159

Scriber JM (2011b). From Emperor moths to Zulu kings: early entomophagy and Charlotte's web of missionary letters. Association for Tropical Lepidoptera notes, June. pp 1–7

Scriber JM (2014) Review: Climate-driven reshuffling of species and genes; potential conservation roles for species translocations and recombinant hybrid genotypes. Open Access. Insects 5:1–61. doi:3390/insects5010001

Scriber JM, Ording G (2005) Ecological speciation without host plant specialization: possible origins of a recently described cryptic *Papilio* species (Lepidoptera:Papilionidae). Entomol Exp Appl 115:247–263

Scriber JM, Larsen ML, Allen GR, Walker PW, Zalucki MP (2008) Interactions between Papilionidae and ancient Australian angiosperms: evolutionary specialization or ecological monophagy? Entomol Exp Appl 128:230–239

Scriber JM, Eliot B, Maher E, McGuire M, Niblack M (2014) Adaptations to "thermal time" constraints in *Papilio*: Latitudinal and local size clines differ in response to regional climate change. Open Access. Insects 5:199–226. doi:10.3390/insects5010199

Smith JE, Abbot J (1797) The natural history of the rarer Lepidopterous insects of Georgia. Printed by T. Bensley, London

Tyler HA, Brown KS Jr, Wilson KH (1994) Swallowtail butterflies of the Americas: a study in biological dynamics, ecological diversity, biosystematics, and conservation. Scientific Publishers, Gainesville, FL, p 376

Mark Scriber (and most of his students) has chased and observed swallowtail butterflies during all of his career at Cornell University, Wright State University, University of Wisconsin at Madison, University of Queensland (Australia), University of Florida (McGuire Center), and Michigan State University (MSU). Over these years, he has found many sources of funding for his research, even including a primarily administrative position as chairperson of the Entomology Department at Michigan State (1986–1997). He subsequently accepted an "un-endowed chair" position at MSU and for the recent two decades has found this and collaborative research with several universities even more rewarding. His butterfly lighthouse displays mementos and insect stamps. However, most satisfying has been the three-story lakeside tree house on Waikiki Street that he recently built for his grandchildren at his Aloha home in northern Michigan.

Part IV
Natural History

...the very fact of our discussing these matters implies curiosity, and curiosity in its turn is insubordination in its purest form.
V. Nabokov, *Bend Sinister*

Of course good science requires curiosity and careful observation; everyone knows that. What is not as widely discussed is that curiosity also entails a good dose of rebelliousness. After all, what fun would science be without the possibility that you might find the real story when everyone else has been fooled? This certainly applies to the best natural historians among the lepidopterists. These are the folks that look a second time and a third time before they see what others have not: that caterpillars can sing to ants, or fling their frass, or that the most bizarre, flightless moths in North America would be hiding not far from major urban centers.

MLF

Leopard moth. Illustration by Angela Hornsby.

Chapter 11
Butterfly Reflections in Thirds

Phil DeVries

Preamble The editors of this volume asked contributors to offer personal narratives related to the study of Lepidoptera, in my case butterflies. I have studied tropical butterflies for a long time and in many locations. Early on, butterflies influenced the paths I chose in life, and they have remained part of my philosophical rudder. My memory swarms with tales that include butterflies, often in context with other people. The difficulty has been to choose which memories might be amusing to an unseen audience. The chronicle here evolved during fieldwork in China (August 2014) from where I am writing this into a trio of recollections that influenced my development as a field biologist. Much of what I have written happened before cell phones and personal computers, during a time when "R" represented a letter in the alphabet and a rating for sexy movies. Let me begin by quoting a book title by the novelist and lepidopterist Vladimir Nabokov, *Speak Memory*.

Reflection 1: My First Time Inside Tropical Forest

In early 1976, I took my first solo Costa Rican field trip. On the advice of Luis Diego Gomez (the director of the Museo Nacional) I drove an ancient Willys Jeep with canvas top and doors at a top speed of about 50 km/h from San Jose to the CATIE agricultural station in Turrialba. I arrived late afternoon, and with the barest rudiments of Spanish gestured my way to the administrators, was then shown a room where I would stay for five nights. Away from the lights of the town and surrounded by bits of forest, I was thrilled by the insect life that gathered around the light above my door that night. Life was good. Next morning I was told about a trail

P. DeVries (✉)
Deptartment of Biological Sciences, University of New Orleans, New Orleans, LA 70148, USA
e-mail: phil.devries@gmail.com

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_11

that descended and terminated on a rocky bank of the roaring Rio Reventazon. So I walked slowly up and down that trail for several hours. There were lots of butterflies. Although I managed to net one occasionally, most avoided capture by darting off the trail into the forest. Let me be clear about this because this is important: those butterflies went *off the trail* and *into* the rainforest interior (Fig. 11.1). Numerous people, including those from CATIE, had repeatedly warned me about the legions of vicious snakes that waited in the forest to inject toxins deep into the flesh of the unwary. A single bite would cause horrific scars, loss of limbs, digits, eyesight, internal organs, and the most painful death imaginable. They said they knew about this, they had seen the results, they had heard stories, and being bitten was inevitable. Consequently a constant nagging little voice began whispering to me, "Do not go there, Phil! Stay on the trail." Heeding the voice I continued to lumber up and down the trail, often pausing to watch butterflies that were out of my reach. These accounted for a great deal of the species—the forest satyrines, ithomiines, riodinids, lycaenids, and others.

That very day one butterfly changed my perception of the world. Along the trail individuals of *Cithaerias pireta* often glided just above the ground for a short distance, then always veered into the forest. Anchored to the trail I watched their transparent wings and flashing rosey patches from afar as they cruised along the forest floor, frequently settling in small patches of light. Temptation grew stronger to collect a *Cithaerias,* but the voice reminded to watch safely from afar and wait for the right time on the trail. My imagination was conflicted by desire

Fig. 11.1 Forest trail in lowland rainforest, Parque Nacional Corcovado, Costa Rica. (Photo by Phil DeVries)

Fig. 11.2 *Cithaerias pireta* (Nymphalidae: Satyrinae) feeding on juices of a fallen fruit of *Dipteryx panamensis* (Fabaceae) in Costa Rica. These butterflies glide along the forest floor and entice biologists to walk off the trail. (Photo by Phil DeVries)

and some form of dark fear. Deep yearning to collect *Cithaerias* won the conflict, but at the same time dictated that I was to walk among invisible serpents. With a mind focused by adrenaline I held my breath and stepped into the forest. I crept slowly, ever so slowly toward an individual sitting in a small pool of light. Judging the range I swung the net. I missed. Adrenaline ebbed and gave way to realization—I was in the forest 10 m from the trail. I scanned the dappled light for snakes, but saw none. The little voice started to whisper, but was silenced when I saw more *Cithaerias* a short distance away. After numerous attempts I finally managed to collect one, and the trail was somewhere distant. Taking stock of my surroundings I found I had more curiosity about inside the forest than dread. Thinking about my dilemma fueled by rumors and hearsay a short time ago I laughed aloud at myself, the music of life. The next 4 days inside the forest were glorious. Life was now grand. I had escaped my shackles of the trail because of a butterfly, and from that time onward I have seldom heard that whispered voice again (Fig. 11.2).

Reflection 2: And Mine Eyes Were Opened to the Glory

In 1985, I received a Smithsonian Tropical Research Institute pre-doctoral fellowship to explore the association between ants and *Thisbe irenea* (Riodinidae) caterpillars on Barro Colorado Island, Panama. Despite their tremendous neotropical species richness, very few riodinid life histories were known at the time. What was known about *Thisbe* was in a paper by Bob Robbins and Annette Aiello, namely that on Barro Colorado Island the caterpillars fed on *Croton bilbergianus* (Euphorbiaceae) and associated with ants. Since I had never before worked on any riodinid butterfly, I was flying blind. In fact, my fate as a doctoral candidate was in the balance, so I was jumping off a building hoping someone would offer me a parachute. That someone turned out to be *T. irenea*.

I spent the first month walking all over Barro Colorado Island marking individual *Croton* plants, learning to find *Thisbe* caterpillars, and observing ant behaviors as they tended both caterpillars and extrafloral nectaries on *Croton* leaves. I also spent some dusk-to-dawn sessions in the forest sitting on a folding chair, slapping mosquitos and picking ticks off my clothes while witnessing parts of the *Thisbe* story unfold. This fieldwork established that caterpillars were found only on sapling *Croton* plants, that ants always tended them, and young instars fed throughout a 24-h period, but larger caterpillars typically fed only at night. Ants constantly drummed their antennae on a dorsal area of a caterpillar that would occasionally extrude one or both of the tentacle nectary organs, offering ants a drop of clear secretion, then quickly retract them. The ants continually solicited secretions, often riding astride the caterpillar as it moved from one place to another. When a caterpillar moved along a stem to or from a leaf, it also employed two other sets of organs: the anterior tentacle organs and the vibratory papillae. When the tentacle organs were extruded, they stimulated a behavioral change in the ants—the tending ants became excited and aggressively wary of anything moving in the vicinity of the caterpillar. The vibratory papillae beat constantly when a caterpillar moved or was being tended by ants. Only later when examining them under powerful magnification did I realize they were sound production organs—something unknown from any caterpillar. My subsequent 11 months on Barro Colorado Island were spent exploring the role each caterpillar ant-organ played in the symbioses between *Thisbe* and ants and comparing them to other riodinid caterpillars. Writing it up for my doctoral dissertation, I realized the parachute had been provided.

That year plus a subsequent one as a Smithsonian postoctoral fellow I lived in close association with riodinid caterpillar–ant symbiosis. Starting with *T. irenea* and extending my observations outward showed that riodinid life histories were as diverse as the adult forms one saw in books or museum specimens preserved on pins. Field research on riodinid caterpillars and ants opened a different world to me and revealed generous examples of how their associations evolved in wonderfully varied ways. These caterpillars have various organs that seem to produce volatile chemicals that alter ant behavior and other organs that provide food secretions ants greedily imbibe—a payment for protection against insect predators (Figs. 11.3 and 11.4). I found that caterpillars frequently feed on plants

Fig. 11.3 Caterpillar of *Thisbe irenea* (Riodinidae) being attended by *Ectatomma ruidum* ants (Formicidae) in Panama. These ants protect *Thisbe irenea* caterpillars against predaceous insects in exchange for food secretions. (Photo by Phil DeVries)

Fig. 11.4 Caterpillar of *Thisbe irenea* (Riodinidae) as a prey item of a vespid wasp in Panama. This particular caterpillar was found by the wasp without a guard of symbiotic ants. (Photo by Phil DeVries)

bearing extrafloral nectaries, and in addition to feeding on leaf tissues, they drink extrafloral nectar and gain growth benefits from it as well—always under a constant guard of ants. Everywhere my research has taken me I found a general phenomenon that: all caterpillars forming symbioses with ants produce calls, and caterpillars that do not form such symbioses are mute. Moreover, the ability to produce calls has evolved multiple times in butterflies. I found that some riodinid caterpillars form symbioses with a number of distantly related ants, while others associate with a restricted group of closely related ones. Later I documented that in many habitats all over the world, caterpillars forming symbioses with ants do so only with ant taxa that regularly harvest secretions from plants and other insects. The lagniappe is that together these observations illustrate how distantly related groups of plants and insects are intimately linked through symbioses involving ants and secretions. I have observed many other life histories in these butterflies, each revealing variations on the symbiotic theme. What a system for a naturalist to work on!

Long ago I began a journey guided by *T. irenea,* one that has taken me to surprising places and taught me to keep discovering new caterpillar–ant symbioses. Over 20 years after my initial work on Barro Colorado Island, I realized that *Thisbe* provided links for me to see the natural world in a different light.

Reflection 3: The Road to Tropical Butterfly Diversity

Everywhere I have travelled people seem impressed by the height, shape, life story, and the grandeur of large trees whose canopies can mask the sky. Everyone who walks into a tropical rain forest displays a similar response. Moments after getting their bearings they look upward to assess the canopy, particularly when trees physically dominate the landscape.

I have been looking at the forest canopy for quite a while. During my rural childhood I climbed tall oaks, maples, and pines just to see what it was like up there. I built tree houses, and was always eager to challenge anyone to who could climb the highest. The forest canopy always made me wonder if animals in the treetops differed from those in the understory. Exactly when I became serious about testing for differences between canopy and understory butterflies is unclear, but it certainly had to do with the company I kept in late 1979, early 1980. At the La Selva Biological Station in Costa Rica I was part of an early wave of biologists who being young, competitive, and without regard to mortality, started climbing ropes into the rainforest canopy. We looked around, built platforms in various trees, maybe sampled some plants, and enthused about the potential. Let me be honest; it was grand, exciting fun, and yielded impressive tales to tell later.

The principal instigator who showed us the ropes, so to speak, was Don Perry. Don constantly asserted the canopy was an unexplored biological world that differed from the understory. Reasonable enough, but I often bantered with him about what data were available to support this, beyond a few observations on epiphytic plants. From these jovial exchanges I began thinking about how to test the potential canopy–understory difference using butterflies. The trick was how to sample in both areas simultaneously. Initially I considered two people armed with butterfly nets, one in the canopy and the other in the understory. A silly idea because the canopy person's working area was severely limited by being tied to a rope. I also thought that taking a page from the bird watchers might work, but as there were no field guides in those days, using binoculars to identify butterfly species was nebulous at best. I kept mulling the problem over until I realized that combining rope climbing and my traps for understory fruit-feeding nymphalids might be the solution. The traps would not sample nectar-feeding butterflies (papilionids, pierids, hesperiids, riodinids, lycaenids, and some nymphalids), but at least I could sample in two places at once. Fruit-feeding nymphalids just might answer my question and into the bargain minimize the sampling bias of using hand nets. After some discussion and planning, Don agreed to assist with my trapping scheme; he helped shoot lines, directed, and laughed as I climbed and installed lines over canopy branches. After several days canopy and understory lines were installed on five trees. I baited them to start the study, and 10 weeks later I had sampled 182 butterflies in 46 species, and some from the canopy were quite rare in museums. Then I left to start graduate school at the University of Texas. Much later, while finishing my PhD and first Costa Rican butterfly book, I published a small paper on butterfly stratification based on those samples. While the sample size was small, basic analyses suggested that butterflies sampled from canopy and understory differed in interesting ways. Later I came to appreciate that this was just the tip of the iceberg.

The next few years were spent working mostly on caterpillar–ant symbioses and my Costa Rican riodinid book. Nonetheless I still thought about canopy and understory butterflies, and at some point realized that longer-term sampling was important. Reprise came in 1991 near San Vito de Java, Costa Rica when Paul Ehrlich's group asked me to help build a biological station (literally from the ground up) at Las Alturas. My old boss Luis Diego Gomez (the head of the nearby Wilson Botanical Garden) agreed to help with local things administrative and bureaucratic. So after some discussion I accepted the Ehrlich-group offer, and among other things, we agreed I would set up a 1-year trap study to sample canopy and understory butterflies at Las Alturas and later another at Jatun Sacha, Ecuador where I had worked previously. Those were interesting times indeed. The memories of the adventures and the people I met could fill volumes. That was when I first met Harold Greeney in person. He came to work with me at Las Alturas, and later we shared many field experiences in Ecuador and beyond—and what stories could be told! Perhaps Harold will write them before I do. The important point here is that the Las Alturas study flopped but the one at Jatun Sacha flourished. Trapping for the first week of every month over a year provided a glorious sample of 6690 individuals and 130 species and revealed strong patterns about canopy and understory diversity only hinted at by the first Costa Rican study. The investigation also suggested other patterns yet to be explored and formed the basis of a solid publication. My butterfly trap studies had begun in earnest, and there were more on the horizon.

The Jatun Sacha study made me think about two things: 1 year of trapping seemed only a glimpse into the dynamics of species diversity in time and space, and as Jatun Sacha was a mosaic of disturbed forest, I wanted to know if butterflies in an intact Amazonian forest showed similar patterns. And so it began all over again, this time down the Rio Napo to the then magnificent forest at Garza Cocha where things really started to happen. As an assistant professor at the University of Oregon at the time, it was a grand feeling to realize that those trap studies were the largest continuous monitoring study on species abundance distributions ever assembled for any tropical butterfly community. It was strong stuff that inspired confidence. But the world of federal funding agencies had other opinions. Despite the consistent disinterest in my proposals for long-term trap work, I was determined to set up and maintain other comparative studies. Stubbornness coupled with a lot of field help paid off (Fig. 11.5).

Of the six trap studies I instigated in Central and South America, the touchstone was at Garza Cocha, Ecuador. This is where monthly sampling progressed from 1 to 5, to beyond 10 years, always following a time series that pulsed along on schedule. That study opened the world of tropical butterfly diversity to me. It demonstrated robust differences between the canopy and the understory (they are separate communities!), it revealed significant changes in species diversity in space and time, and provided the first real insights into seasonal cycles of tropical species diversity, and the density dispersal, and longevity of Amazonian butterfly species within in-

Fig. 11.5 A trap for sampling fruit-feeding nymphalid butterflies in lowland Amazonian forest at Garza Cocha, Ecuador. Long-term studies using these traps have been important to understanding tropical diversity in space and time. Phil DeVries and Russ Lande are depicted for scale. (Photo by Phil DeVries)

tact forest. Given the circumstances under which it was conducted, I remain astonished that it was possible to continue the Garza Cocha study for so long. Although years ago the odysseys at Garza Cocha and elsewhere ended, I can gladly report the study at Tirimbina, Costa Rica, still remains. It has continued for over 10 years, produced a wealth of new discoveries, and it will likely become the next long-term milestone for Neotropical butterflies. It is also exciting to learn that trap studies are now emerging from various forest localities in Brazil. These will provide a great deal of important comparative information on tropical diversity.

My trap studies materialized because a number of people born to do fieldwork were foolish enough to listen to me. I confess to conscripting these younger biologists by convincing them that working (mostly without compensation) under primitive conditions would be an adventure, change their lives, and at the same time be lots of fun. I fully understood that sampling with traps on a strict schedule was often inconvenient drudgery and certainly not fun. Yet somehow as teams we managed to gather those unique, hard won data. Today most of those conscripts are professional biologists, and I would like to think that living the trap life did change their lives and now they pass on the fun of fieldwork to their students. A partial catalog of those magnificent scruffy colleagues includes: Isidro Chacon, Caroline Dingle, Casey Dunn, Chris Funk, Harold Greeney, Rodney Guerra, Ryan Hill, Eric Schwartz, Jarol Vaca, Tom Walla, and a multitude of local people. If in the future any one of them needs help from an aging field biologist, I do hope they will think of me.

Now it is time to tell tales from the other side of the traps. Conducting fieldwork seems easy to me. But publishing scientific papers from the riches of long-term trap data often requires sophisticated analytical expertise. That is not my strength. Since the very first trap study Russ Lande consistently encouraged my fieldwork and suggested novel ways of thinking about the natural world. He managed to impart an appreciation of why numbers really matter, particularly at the intersection of theory, analysis, and hard data. Although I struggle with analyses, I have come to appreciate that intersection as a beautiful place to be, like in the middle of a tropical forest. Imagine that! I have been fortunate to collaborate with theoreticians and statisticians who appreciate that data from the real world are important to ecology and evolution. In addition to Russ, the talents of Steinar Engen, Jim Fordyce, Vidar Grotan, Lou Jost, Bernt-Erik Saether, and Jarle Tufto lifted the trap data to levels I had not imagined from a field perspective. Not infrequently I witnessed heated interactions between these sagacious collaborators about who had the correct answer or best analytical approach to a particular problem. Having seen these behaviors among field biologists, I knew when to keep my head down. But I have often wondered what would this group of theoreticians and statisticians be like as butterfly trappers in the forest?

From the first trap study in 1979, the questions posed by fruit-feeding butterflies dictated that studies evolve to be of longer duration, have better sampling design and analyses, and include more people—all who became trapping enthusiasts. Each trap study added new questions, new perspectives, and together they form a comparative data set that really helps us understand tropical diversity.

Despite my difficulties in obtaining funding for long-term trap studies, I believe the work on fruit-feeding nymphalid butterflies has proven important for understanding tropical diversity and the evolution of life on earth. Perhaps someday societal perceptions will change and studying tropical diversity for its own sake will be in favor. But until then my money is on the symbioses between stubborn field biologists, theoreticians, and statisticians to get the job done. Now to me, that makes a beautiful story.

CODA: In a world frantically dependent on communication technology, not only can you know what “social media friends” do at every waking moment, but even better, one can find information on just about anything from anywhere in the world. With a few keywords and keystrokes on the computer, a myriad of websites will appear within moments, each with pictures and information about butterflies. While some web information can be a little left of trustworthy, the global network unifying information that everyone contributes to and uses is still evolving. This is a good thing. Just like any working biologist, I too utterly depend on web resources and digital tech to do my work and communicate with others. But it does seem like the study of wildlife by many university inhabitants has increasingly become something to vicariously look at or study online rather than meet on its own organic terms. Perhaps this is an inevitable development, but I suspect distance learning will be insufficient for some students of biology. Rather, for them knowing organisms in the wild will become one of life’s great pleasures. Accordingly, let me close with a favorite phrase that I believe was coined by the Brazilian novelist Jorge Amado, “There are no vacations in the school of life.”

Acknowledgements Many people have influenced my work on Lepidoptera and helped navigate the way forward. I hope those named in the imperfect narratives will recall situations, and perhaps smile. Butterflies are good botanists and to know something beyond their Latin names, I think you need to find caterpillars, and for that you need to know plants. Thanks to Robin Foster, Al Gentry (deceased), Luis Diego Gomez (deceased), Bill Haber, Dan Janzen, Larry Mellichamp, Luis Poveda, and Warren Wagner (deceased) for setting me on that path. For discussions on butterflies that I still think about today I acknowledge Phil Ackery, George Austin (deceased), Peng Chai, Robert Dudley, Tom Eisner (deceased), Larry Gilbert, Carla Penz, Mike Singer, Gordon Small (deceased), Jeremy Thomas, John Turner, and Dick Vane-Wright. Finally I thank my wife and colleague Carla Penz (The Mighty Phlea) for support, criticism, enthusiasm, and understanding over the last 20 years, in addition to patience beyond category.

Phil DeVries is a tropical field ecologist and naturalist who has conducted research in many tropical habitats and countries. He received a Bachelor of Science (BS) from the University of Michigan, spent 5 years in Costa Rica (3 years with the Peace Corps), and then received his PhD from the University of Texas at Austin. He has published papers on the natural history, behavior, ecology, evolution, and species diversity of butterflies and two classic field guides on Costa Rican butterflies. His work on Riodinidae and fruit-feeding nymphalids has strongly influenced our understanding of tropical butterfly symbioses, community ecology, and dynamics. Phil continues to be tropically peripatetic. He has received a MacArthur Fellowship, Fulbright Fellowships, a Guggenheim Fellowship, and a Rolex Award. A number of insect taxa carry patronyms, and recently minor planet 89131 Phildevries was named for him. When not in the field or working on butterfly-related projects, Phil cooks, makes charcuterie, listens to improvisational music, reads science fiction, and chases ambient light to make black and white photographic portraits and street scenes. He also tries (quite successfully) to laugh a lot everyday.

Chapter 12
It Should Have Been Called a Moustache

Harold F. Greeney

Stories you say? A significant moment from the field? Hmmm. Countless stories, numerous, humorous, tragic, magic, and fascinating, simultaneously clogged my creative ducts the moment I was invited to contribute to the present book. Sadly, some experiences, such as a particular incident involving a terrible night's sleep on the rocky soil of the Sonoran Desert, a gallon-sized can of ranch-style beans, and two dogs with incredibly vile dietary proclivities, must forever remain as orally transmitted traditions. (If you know the story, you are cracking up right now; if you do not, you will hear it eventually, and if you were there, you are fighting dry heaves). Of those stories suitable for general consumption, we will save the dramatic and the comedic for future campfires, lean-tos, base camps, black lights, and rainy days in the field. I have chosen, instead, a single monumental day, now more than two decades in the past. It is a day I will never forget, a story I have shared during many talks, and one from which I continue to draw inspiration, amusement, and even wisdom.

Before we begin, however, a bit of backstory may help readers interpret the importance (to me) of the story to follow. I have always loved nature, apparently even before I have memories, based on the number of half-eaten cockroaches my mother claims to have found in my diapers. The margins of my Peterson's Field Guides are filled with annotations in my father's handwriting where he entered my field notes before I was able to write them legibly myself. I was born a collector. If I could find more than two of anything, I started a collection and spent endless hours sorting, comparing, and organizing each of my collections into similarity-based groups: rocks, leaves, bottle caps, shells, skulls, coins, stamps, and (of course) insects. So, not surprisingly, I was thrilled when, in 1986, a Boy Scout service project helping the elderly move furniture led to the discovery of two enormous cabinets filled with butterfly specimens in the upstairs room of woman in need of our help. On that fateful day, I met the disgruntled mother of Phil DeVries who was ruing the day she agreed to store her son's butterfly collection while he explored Costa Rica. Upon

H. F. Greeney (✉)
Yanayacu Biological Station, Napo, Ecuador
e-mail: antpittanest@gmail.com

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_12

discovering what the ill-placed furniture contained, I abandoned my fellow scouts to their work and instead barraged this poor woman with an ecstatic stream of questions concerning, what I thought was, her butterfly collection. DeVries' mother explained the collection's origin and, much to my delight, invited me over to meet her son who, fortuitously, was scheduled to be home for Christmas that year. A few weeks later, I dined at the DeVries household with a field-worn Phil who had begrudgingly agreed to talk to "this nice young man who seems *really* interested in bugs." This was, at the age of 15, my first step towards a lifetime of tropical adventure. Another important, and as you will see topical, fascination of my youth concerned the creation of things out of folded paper: airplanes, origami, and (to my little sister's detriment) spit-wads. When I discovered that the caterpillars of skipper butterflies build leaf shelters out of their host plants, spit-wads and airplanes were forgotten. Living insects inside the house were frowned upon by my mother after the "accidental" escape of hundreds of fireflies in my room one night, so as a child I spent much more time finding caterpillars than actually rearing them through to adults. I reveled in the combination of detective work and outdoors skill that this required. Then came high school, college, and girls, the latter of which put a temporary damper on my propensity to talk about how much I loved bugs. It was not until around the time this narrative begins that I really began to bring caterpillars back from the field and rear them.

The day in question (October 12, 1993) began like any other at that time in my life. I woke up 2 hours earlier than the tourists whom I was going to guide that day, having Jedi mind-tricked them into believing that their enormously expensive trip to Amazonian Ecuador would be greatly enriched by sleeping in. This took little convincing after the previous day's "death march" of 8 h with a packed lunch through sweltering heat and boot-sucking mud, undertaken in order to show them what they paid for: tropical nature at its finest. I forget now the number I threw out when a mud-covered tourist asked how far we had traveled during those 8 h, but I know I tried to make it more impressive than the 4 km it was. In any case, as I fumbled around in the predawn for my boots, binoculars, butterfly net, and kill jars, I could hear my fellow Jedi doing the same through the thin bamboo-slat walls that separated our rooms in the guides' quarters of the tourist lodge for which we worked. On that morning we (myself, Tom Walla, and Mitch Lysinger) had yet to recognize that we had already been out-jedi'ed by Phil DeVries, who had unscrupulously Tom-Sawyer'ed us into running a canopy-understory butterfly study in our "spare time" while working full time as jungle guides. After a quick rendezvous at the kitchen for a cup of tepid instant coffee, we each dashed off in our assigned directions to check for butterflies captured during the past 24 hours and to "freshen" up the bait with rotten bananas (which still prevent me from enjoying anything remotely banana flavored). The fact that each of us would take an hour to travel the same paths which had previously disheartened our tourists, plus an additional kilometer or two, has remained our little secret (until now). We were fresh out of college, still eager to learn, and young enough to not notice the snow job DeVries had pulled. About the time we were half-way done, it began to pour, as only a tropical rainstorm can. Air became sheets of water; mud became quicksand; once-solid, exposed-root footholds became our worst enemies (what Mitch referred to as “real ass-busters”). Somewhere, on another continent, DeVries was enjoying a Starbucks’ grande-double-caramel-something-or-other, his feet on the desk in his climate-controlled office, leisurely perusing the thousands of butterflies we had already shipped home from previous months. We did not care. This, this was tropical nature!

After trap-butterflies were sealed in glassine envelopes and put in a dry box, there was just time to rinse off in the water pouring off the roof of the guides’ cabin and put on dry(ish) clothes before sitting down to breakfast with our tourists. While none of us had been running wild in the jungle for more than a year at that point, somehow it was not hard to find an endless stream of entertaining stories to occupy our groups. After breakfast, another day of eager exploring and learning, while occasionally remembering to share a few easily digestible facts with the sweaty, repellent-soaked, tourists who trailed despondently along behind us. Enough preamble and scene setting, onto the real story.

So, as I mentioned, it is 1993 and I am living in a bamboo, thatched-roof hut in the Ecuadorian Amazon. I have fulfilled my promise of butterfly trapping to DeVries, and my tourists are either asleep or boozing it up in the bar. Mitch is listening to, and memorizing, bird songs on his walkman (told you it was a long time ago). Tom has wandered out into the jungle in search of a bushmaster rumored to be sleeping in a hole somewhere along one of the trails. I can finally sit down with my caterpillars, most of them skippers, which I am rearing in small plastic cups with snap lids that are stacked in neatly labeled rows on the shelves in the guides’ cabin. I have in front of me a fourth instar caterpillar of *Telemiades antiope* (Fig. 12.1). In my field book, I am carefully recording the shape, color, size, and behaviors of my subject. In particular, I spend an inordinate amount of time slowly opening and describing the architecture of its leaf shelter; a carefully excised portion of the leaf margin which the caterpillar then laboriously silks into the desired position to form a tent-like or pocket-like shelter. As if it were yesterday, I remember staring at the caterpillar’s rear trying to recall the technical jargon for the semi-hardened plate that covers the dorsum of the last abdominal segment (the aptly named anal plate). Unable to remember, I decided ass-shield was good enough for field notes. At that moment, however, as I watched in fascination, the caterpillar’s anus slowly unpuckered and a perfectly formed, grenade-shaped ball of frass (bug shit) appeared (Fig. 12.2). It paused there for a second, like a drop of dew at a leaf’s edge, apparently sticky enough to not fall off. Then, in an instant, it was gone. Please remember, I was young and, as DeVries would have said, working with a brain which was still blissfully uncluttered by knowledge. I saw no other explanation for the disappearance of the frass other than it had been sucked back into its owner’s rectum. Once again, nature left me in awe. Along with a plethora of jokes that I knew would greatly entertain my peers, this behavior I had discovered set off a tropical storm of questions in my head. Why would a caterpillar do such a thing? Perhaps the nutritional quality of its food plant leaves was so poor that it had evolved a poop-retention strategy, which allowed it to give it one last go for nutrients. Maybe it was water retention. Maybe the behavior depended on relative humidity. Maybe it was not, in fact, a frass ball that I had seen, but a frass-shaped organ of unknown utility which was yet to be described in caterpillars. My pen could barely keep up with my mind as I poured out question after question and proposed answer after answer on the pages of my notebooks. In the middle of my thought, I noticed another frass pellet appear then … gone!! I noted the time, backtracking to estimate the time of its first occurrence. I searched around the caterpillar (sitting on a white notebook) for the pellet. There wasn't one! Aha! They sometimes suck it back in twice! Feeling ecstatic and enormously wise in the ways of science, I spewed forth another series of hypotheses, digging deep into my scant knowledge of the scientific literature to find an explanation. This time, however, I turned the animal so as to have a straight-on view of the phenomenon. Guessing correctly, about 15 min later I was ready, inches from the aperture of interest, as I watched its recycled crap emerge. Again I watched as the puckering exoskeleton stretched and a green grenade slid out, perching delicately on the caterpillar's rear. In the split second that it remained there, I had just enough time to wonder what that curious little brown mustache was. The one which had appeared near the top of the anus just before the frass was produced. Were my eyes playing tricks, or had I just discovered *another* new caterpillar structure! Then, it hit me.

No, it actually hit me. The frass, that is. Now you see it, now you don't. In this case, the don't was punctuated by the tiny grenade bouncing from my furrowed brow and dropping back onto the table. Not for the first time, and certainly not for the last, nature had thrown me a curve ball. In this case, more of a fast-ball shot from the anus of a skipper larva. Although I was disappointed by the fact that my clever one-liners about anal recycling would no longer be of use, I was equally intrigued by this new observation. Pen flew over paper once again and outpoured another series of euphoric epiphanies. As I watched repeat performances late into the night, however, a vague memory began to surface. At that point in my career I had only briefly had a copy of Malcom Scoble's *The Lepidoptera* in my possession. But if memory served, I was, lamentably, not the first to discover that skipper caterpillars not only made origami but they also shot spit-wads. Indeed, skipper larvae, and a few other groups of lepidopterans, will forcibly eject frass from their anus, propelling it away from their location, presumably to reduce the possibility that their excrement can be used by natural enemies as a means of locating them. The anal moustache, sadly a term which has not come to popular use after I coined it that night was, is in fact, the caterpillar's anal comb (hardly an improvement in terms). This structure is a spiny, comb- (or moustache) -shaped structure, which is sclerotized, located just inside the upper margin of the caterpillar's anus. In this position, it serves to hold the extruded frass in position while strong sphincter muscles clench and a small chamber of air is pressurized just inside the anus. A sudden relaxation of the sphincter expels the pressurized air, launching the fecal grenade through the air, often to distances equal to tens of times greater than the length of the caterpillar's body. Thank you Mother Nature for, yet again, providing fascinating (anal) cannon fodder to spice up my growing arsenal of stories to be delivered to bleary-eyed tourists across the breakfast table.

One of the few things that I regret in life is removing those fecal-crazed pages from my notebooks. At the time I feared the shame they would bring me should anyone find them and see how entirely wrong my observations, assumptions, and

Fig. 12.1 A progressive series of photographs showing the steps involved in shelter construction by a fifth instar larva of *Telemiades antiope,* the hero of our story

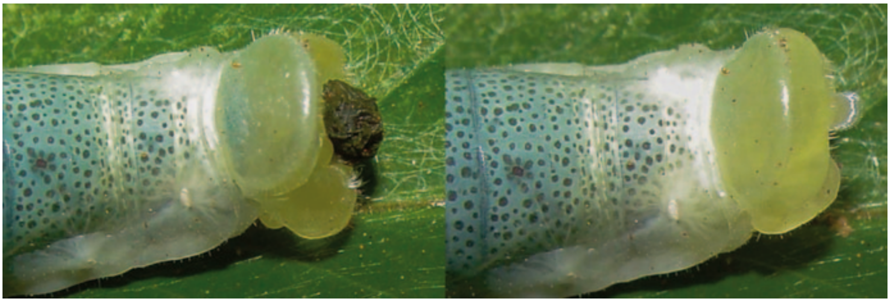


Fig. 12.2 *Left panel:* A frass pellet poised for launch on the anus of a *Saliana* butterfly larva. *Right panel:* Terminal segments of the same individual, moments after frass-propulsion, showing the exposed anal comb (moustache)

ideas had been. Without a doubt, by simply transcribing those pages, I could have entertained you for hours (days) in place of this narrative. This terrible loss to ecology and comedic literature, however, is ameliorated by the fact that my memory of the moment is of such clarity that I can retell it ad nauseam. For me it will always epitomize what science, in particular natural history, is really about. It is discovery. It is wonder. It is passion. It is feeling like you have witnessed something that no one else has ever seen, and now have the power to describe it, understand it, and pass that knowledge on to others. To truly discover and chronicle a piece of the history of nature. And let us keep it honest. It also makes me giggle inside to give a lecture about little creatures with mustachioed anuses that can throw their own shit more than 30 times their own body length.

Harold F. Greeney is a broadly trained natural historian who has conducted much of his research (to date) in the New World tropics. He received a BSc from Wake Forest University where he paid for his education with an Army ROTC scholarship and cheered on the Demon Deacons as a Wake Forest Cheerleader. After several years guiding jungle tours in the Ecuadorian Amazon, he received an MSc in entomology from the University of Arizona while studying aquatic insects in Ecuador and subsequently earned a PhD in ornithology from the University of Wroclaw while

studying the breeding biology of tropical montane birds. Harold is, perhaps, best known as the creator of the Yanayacu Biological Station and Center for Creative Studies on the east slope of the Ecuadorian Andes, a place he called home for nearly 15 years. Harold was among the first recipients of the prestigious Alexander and Pamela Skutch Award honoring his dedication to publishing studies on the reproductive ecology of tropical birds and was recently awarded a Guggenheim Fellowship to help in the preparation of a field guide to the nest and eggs of Ecuadorian birds. Currently, Harold is studying the reproductive and migratory behavior of birds in southwestern USA and northern Mexico while finishing an authoritative book on the antpittas and gnateaters of the world. When not rearing caterpillars or filming bird nests, he dedicates his time to passing on a passionate love of the natural world to his children.

Chapter 13
Collections, Serendipity, and Flightless Moths

Jerry A. Powell

The urge to collect has been described as an affliction that is intractable as any virus, for which there is no immunity or cure. My earliest recollections of collecting, when I was 6 or 7 years old, are of bottle caps and matchbook covers. With the advent of Pearl Harbor and WWII, I was 8, came military campaign ribbons and implements, then postage stamps, and so on. My parents, who never had any interest in collecting, I suppose assumed I would outgrow it and develop a viable career. I believe the collector urge is unrelated to genetic or environmental inheritance. At least it was for me. Oddly, however, I had no particular interest in natural history until age 13 when I was sentenced to a summer class for junior naturalists with weekly field trips, organized by Charles Harbison of the San Diego Natural History Museum. Captivated by Harbie's infectious enthusiasm and the association with experienced bug collector students, my innate collector urge shifted. I had a morning paper route and soon discovered sphingids and tiger moths at liquor store fronts, the likes of which my butterfly collector friends had not seen. I obtained pins and a cyanide bottle from Turtox and began carrying it in a WWII canteen affixed to my bicycle seat. By the end of that summer I was an incurable lepidopterist.

That was 68 years ago; now I am an octogenarian, I get up, do some pushups, put coffee water on and go downstairs to check the moths at my blacklight, record the species, collect any unusual ones, and before breakfast enter the records in a calendar notebook, as I have done for nearly 30 years at this site. After more than 7000 collection dates, I am still getting an average of 3.5 species per year new to the inventory. The discovery of the light brown apple moth in 1996 seemed to be an amazing coincidence to the news media folks, a new insect arrival found by the one person among 35 million Californians who might recognize its significance. But of course with nobody else in coastal California sampling microlepidoptera on a regular basis, I was bound to see it first.

J. A. Powell (✉)
University of California, Berkeley, USA
e-mail: powellj@berkeley.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_13

One of our graduate students once observed, in all sincerity, that I might have become a really successful biologist if I "didn't have this penchant for collecting" (I was about 35 at the time). His assumption seemed unlikely, but there can be no doubt that I have been first and foremost a collector.

Research My research emphases were self-selected and focused on interrelationships of larval host plants and systematics. Topics shifted from sparganothine tortricids and long-term studies of prodoxine moths, yucca biology and prolonged diapause to New World and Australian ethmiids, pine tip *Rhyacionia* with W. Miller, and conifer feeding *Choristoneura* with De Benedictis and colleagues. I then shifted to long-term inventory of Lepidoptera at Big Creek Reserve, Monterey Co., Inverness, Marin Co., and the California Channel Islands.

My most memorable field trip was my first to mainland Mexico, with John Chemsak, when we camped out most of the way in Durango and Sinaloa in July and August, 1964. This was at a time when relatively few gringos had made moth collections in that region. By the 3rd day in Mexico, I became very ill with dysentery and recovered only after John obtained a strong *medicina* from a *pharmacia*, which killed the gut flora. Although weakened, I collected for several weeks in the Sierra Madre Occidental and along the Sinaloa coast with enormous success, nearly every species new to me. This was during the early years of my systematic monograph of New World ethmiid moths. I suspected, based on few museum specimens, that the west coast of northern Mexico would be important to sample in late summer after the rains began. On the 1964 trip, we collected 18 species of *Ethmia*, 8 of them previously undescribed, and all poorly represented in collections. We continued camping into the 1970s, but by the early 1980s, we stayed in motels. Later, based in part on nontarget sampling during the 1964 trip, Chemsak, John Brown, Don MacNeill, Don Veirs, and I collected tortricine moths extensively in Mexico and Costa Rica, which contributed to several systematics studies, including our comprehensive revision of *Anopina* (Tortricidae); 49 of the 65 species we recognized were newly described, including 39 that we had collected.

On one occasion in 1982, Chemsak and I were collecting along a remote, poor road in Guerrero, when we stopped at a seepage with a lot of butterflies at mud. He walked up the road, out of sight, and a pickup appeared. Four or five young men, boys really, each with an automatic weapon piled out. With my knees scarcely able to keep me upright—I actually imagined this was the last day of my life—I tried to explain in my poor Spanish what we were doing there. They seemed dubious, I thought, but finally John wandered back, offered the *jefe* a cigarette, then a *cerveza*, and order was restored. They were *Federales* who told us this road was a frequent route for drug traffic and advised us to find *mariposas* elsewhere. We did.

Serendipity In contrast to directed insect survey, some of the most remarkable discoveries with which I have been involved have been closer to home and unplanned, even fluky. Such finds were simply luck, typically discovered when I was working on an unrelated project or contributing to an inventory. Here are four examples:

***Ethmia charybdis* Powell, 1973** In April 1967, Paul Opler, Paul Rude, and I visited Big Panoche Gorge in San Benito County, CA, an isolated canyon in the arid east side of the Central Coast Range with desert elements in its flora. It had been seldom sampled for insects, and we went because a coleopterist, John Doyen, urged us to, based on his previous visit. The place had poor access, which we underscored by getting our truck stuck trying to come back up a steep, treacherous, sand road, several miles from the nearest telephone. Therefore we spent an extra day collecting. Among species we found were *Epiblema rudei* Powell, which causes stem galls on *Gutierrezia*, as well as several interesting diurnal primitive moths, but the most remarkable discovery was *Ethmia charybdis*, a winter moth. We collected larvae on *Amsinckia* (Boraginaceae), and I stored the collection until midwinter when I found an *Ethmia* had emerged, one which I immediately knew was something I had not seen before. Although describing a new species from a single specimen generally is not a wise taxonomic procedure, in this instance it was a member of a genus for which I had studied all available New World Museum specimens. Moreover, its morphological features were so derived that they forced expansion of the generic characters, having very reduced mouthparts, elongate wings, and extremely long and slender legs, so I included its description in my monograph.

But the story gets more quirky. In March 1970, Robert Dietz IV and I collected additional larvae on *Amsinckia*, this time from Joshua Tree National Monument in the Mojave Desert. There was no emergence that season. In September, I took sabbatical leave to study at the Smithsonian, and I carried the dormant cocoons to be stored over winter in our basement in Alexandria, VA. In late November-early December, a male and female emerged, the latter brachypterous, then the first such example known in New World Gelechioidea. In a stunned, "Eureka!" moment, I realized what I had; a long series of this flightless moth had been forwarded to me for identification several years previously by Dorald Allred at Brigham Young University. They had been collected in pitfall traps during winter survey of the Nevada Test Site in 1960–1961. Neither I nor lepidopterists at the US National Museum had been able to place these short-winged creatures with vestigial mouthparts, even to family, and when describing the male of *E. charybdis* I failed to connect them. With the monograph in press by this time (1971), I was unable to add a description and illustrate the female in detail, but I mentioned it in a footnote and later illustrated it in *Moths of Western North America*.

A chance visit to an arid California canyon, simply because it had little collecting history, yielded the key to unlocking relationships of this weird yet widespread desert winter moth.

***Areniscythris brachypteris* Powell, 1976** I had a long-standing interest in sand dune insects dating back to my student days, when I rediscovered typical *Argyrotaenia franciscana*, a species described by Lord Walsingham, which he collected in San Francisco "on the sand hills" in May 1871. This was at the beginning of his 14-month microlepidoptera collecting odyssey through northern California and Oregon, and we have been trying to recover and identify his species for more than a century. The San Francisco dunes he visited were pretty much destroyed by the 1950s, but I found populations of *A. franciscana* in Golden Gate Park and at Point Reyes north of San Francisco and continued to sample at sand dunes. Other than at

Los Angeles and San Francisco, coastal sand dunes in California for the most part had escaped total destruction because they had no value for grazing and agricultural crops. However, in December 1971, I visited the Oso Flaco dunes near Guadalupe, San Luis Obispo Co., where I found a rich array of microlepidoptera in the 1960s; I was shocked and dismayed to see the extent of destruction of the dune flora by off road vehicles (ORVs). On the spot, I decided to launch an inventory of microlepidoptera at remaining California coastal dunes sites.

Among all sites I visited over the next few years, the most pristine large dune system was Dune Lakes in San Luis Obispo Co., CA, an agricultural preserve used to maintain five small lakes that provide water for field crops to the north. I learned that John Pinto, a coleopterist, had visited the dunes while he was teaching at Cal Poly, San Luis Obispo. I telephoned him in 1972 for contact information to visit Dune Lakes, and at the end of the conversation he asked if I knew much about a small moth running around the dunes; I had no clue. I visited Dune Lakes several times during the next few years to study the behavior and life cycle of this truly remarkable species, and 40 years later, *Areniscythris brachypteris* remains the only North American moth that is flightless in both sexes. It is one of exceedingly few flightless continental species in the world. Several species on oceanic islands are fully flightless, but even those are not as dramatically modified in larval and adult morphology and behavior as is *A. brachypteris* (Fig. 13.1 also see Fig. 13.2 for more moth diversity). Its wings are short and thickened, with rudimentary venation, not functional for flight; the hind tibiae are greatly enlarged, and the tarsi elongated in both sexes. They run on the open sand dunes and when disturbed, often leap 5–10 cm high, enabling passive dispersal by the persistent onshore winds. They dig shallow pits in which they crouch during windy periods and in which they bury themselves at night. The long, slender, wireworm-like larvae live in sand-covered silk tubes attached to various plant species, from which they mine the leaves.

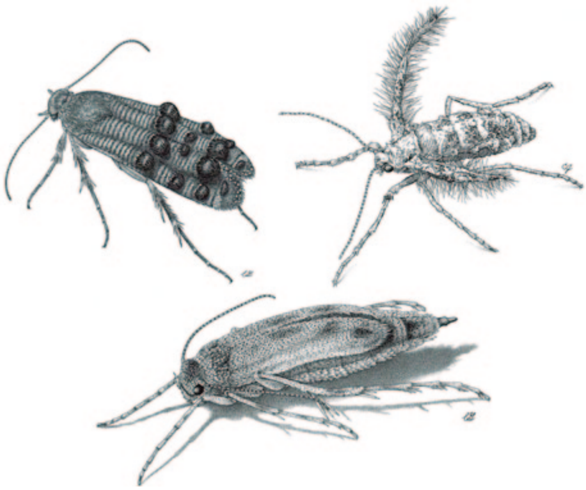


Fig. 13.1 Clockwise from *upper left*: (1) *Lithariapteryx elegans* Powell (Heliodinidae), a diurnal species also on coastal sand dunes of central CA; (2) *Tescalsia giulianiata* Ferguson (Geometridae), a bizarre, flightless female winter moth of the desert east of the Sierra Nevada; (3) *Areniscythris brachypteris* Powell (Scythrididae), the only Nearctic moth that is flightless in both sexes

Fig. 13.2 Clockwise from *upper left*: (1) *Caloptilia reticulata* (Braun) (Gracillariidae) leaf miner of *Quercus agrifolia*. Typical posture of several *Caloptilia* genera. JAP photo. (2) *Adela septentrionella* Walsingham (Adelidae); females ovipositing into floral buds of *Holodiscus discolor* (Rosaceae). (3) *Anatralata versicolor* (Warren) (Crambidae, Odontiinae), which we discovered at two bashed sites just north of UC. The larvae feed in large mines in *Wyethia angustifolia* (Asteraceae); Image by Rollin Coville. Most flown specimens in collections are black, having shed their brightly colored scales. (4) Leaf mine by *Phyllocnistis populiella* Chambers (Phyllocnistidae) in Alaska; JAP photo 1979

Arguably the most bizarrely modified moth in North America, it was a chance discovery prompted by ORV destruction of its habitat.

Tescalsia giulianiata **Ferguson, 1994** The late Derham Giuliani was an extremely knowledgeable, hermit-like naturalist who lived for many years in Big Pine, Inyo Co., CA. His expertise on a wide array of plants and animals was sought by biologists of diverse interests. In 1976, he stuck his head in my office doorway during one of his annual visits to the San Francisco Bay Area, which without fail reaffirmed his disdain for city and freeway life. Typically when he showed up with a question, we could not answer it, and this time was no exception. He produced a flightless moth he had collected in Deep Spring Valley, east of Big Pine, in December, 1973. I could not identify it, even to family, because (a) I was unaware of any moth known to be active in December in northern Inyo County; and (b) the specimen, a female, has peculiar straplike, bristled forewings, as well as vestigial hind wings and mouthparts. In comparison to described winter geometrids (e.g., *Animomyia, Phigalia,* and *Operophtera*), this species shares reduction of tympana but has uniquely derived forewings, rather than simply reduction of them. She has long, slender legs, with which she climbed quickly in shrubs, with acrobatic movements from twig to twig, but she seemed awkward on sand.

Despite my ignorance of winter moths and of Geometridae specifically, I felt compelled to learn more about this unique species. During 1976–1982, I organized

December trips to Big Pine, with Doyen or John De Benedictis and assisted by Giuliani. However, after returning empty-handed—like zero insects—recruiting people to endure this mania became a challenge. Nonetheless, we tried to locate additional specimens and corresponding males. Temperatures at Big Pine typically were below freezing soon after sundown, but often reached daytime highs of 35–40 °F, so, being Californians, we assumed this moth must be diurnal. We searched by visually scanning open-sand sites, sifting and lightly brushing the sand surface for 2–8-h periods and blacklight trapping overnight, all to no avail. We also deployed a few pitfall traps, and after capturing two females of the new species in 1978, we increased the numbers of traps. One of the two females taken in alive laid 10 eggs singly in the sand. After 8:16-h refrigeration cycle for several weeks, tiny inchworms began emerging, confirming the mystery moth as a geometrid. Unfortunately, they did not feed on the synthetic diet or foliage we offered. Finally, in 1982 we succeeded in identifying the males in four colonies that Derham had discovered. Their flight, which did not begin until well after dark, occurred at temperatures of 28 °F and below, associated with calling females.

Although the Lepidopterists' Society editor deleted the word "extraordinary" from our original title, I disagree; this is the most bizarrely modified winter geometrid in North America. I was pleased that Derham lived to see it finally published. But his original, keen-eyed discovery had been misleading, a nocturnal species wandering in the daytime on open sand, rather than climbing in a shrub to broadcast pheromone at night.

Longest Diapause and Development, 1970–2000 My interest in yucca moths and their ability to extend diapause dates back to March 1961, when I split some 1960 inflorescence stalks of *Yucca* [now *Hesperoyucca*] *whipplei* in San Diego Co. and found a lot of living larvae of *Prodoxus*, even though adults were active concurrently at the site. I had read in C. V. Riley's 1892 report that adults of this same species, *P. cinereus,* "issued from the same stems during… May 1888, 1889, and 1890." This intrigued me no end (literally), and I initiated a study of the interrelationships among *Hesperoyucca whipplei* and its four species of prodoxids with R. A. Mackie. With the aid of Chemsak and Opler, we made collections of yucca stalks and opened fruit from widespread localities in midwinter and early spring to determine the emergence pattern. Basically, I found that if conditions (temperature, rainfall) are optimal, irrespective of photoperiod, all or nearly all larvae undergo diapause development, and adult emergence occurs synchronously with the bloom period one year after larval development. If conditions are less than optimal (e.g., drought, held over winter indoors) many larvae maintain the diapause state, even though sometimes sibs in the same stalk develop and emerge successfully. I found the proportion maturing could be controlled from 0 to nearly 100 % by modifying temperatures over winter. After 2–6 or more years, prolonged diapause could be followed by successful development and emergence during a period of a few weeks corresponding to yucca flowering.

Along the way, I tested collections of overwintering larvae of several other species of yucca and their *Prodoxus* and found in general the same pattern prevails. In

April 1970, Dietz and I traversed the Mojave Desert recording flowering and moth emergence patterns of several yucca species following an exceptionally dry winter. At many localities we found only low numbers of plants had developed inflorescences, and most of their *Prodoxus* remained in diapause. During feeding, *Prodoxus* larvae cause discoloration of surrounding inflorescence tissue, which hardens as the inflorescence dries. During winter and later years the hardened case protects larvae from desiccation. At Kyle Canyon in the foothills of the Spring Mountains NW of Las Vegas, many *Yucca baccata* that had bloomed in 1969 had incredible densities of larval *Prodoxus y-inversus*, and the fruit was hardened into coalesced woody capsules. We gathered about 20, which, it turned out over the next 30 years, yielded >520 moths.

For the 1970–1971 winter, preparing for sabbatical leave, I moved all my yucca moth collections to a constant temperature room (20±2 °C) which would prevent development. After I returned, I stored the yucca lots in an open shed in Contra Costa Co., CA, an inland site that provided much colder winter than at Berkeley. There, 12 *Prodoxus* developed and emerged in June 1972, along with >100 parasitoid wasps (*Sycophila* [= *Eudecatoma*], Eurytomidae). Shaving off some of the woody material several times during 1974–1984 revealed large numbers of *Prodoxus* still viable in their tightly sealed cocoons, so I continued to deploy the 1969 seedpods in varying winter exposures.

I am certain that among all surprising events in insect biology I have witnessed, none left me as astonished as a moment in April, 1985. Following a 4-day field trip, I checked my outdoor cage and was amazed to see about 20 *P. y-inversus* milling around, some as mated pairs, in the clear plastic emergence tube protruding from the box holding my *Yucca baccata* collection! My first reaction was there must be some kind of label mistake, or maybe one of our comedic graduate students had brought in yucca pods…. but in a few seconds I collected my wits… the current students were barely past toddlerhood when that collection was made in 1970; they had no idea what this was. I was looking at dozens of moths having emerged within a 4-day span from yucca pods they had fed upon as larvae in 1969, 16 years ago! In fact, the emergence continued for 2 weeks, with a total of 120 individuals completing metamorphosis within 16 days. This was the maximum time known for numerous individuals of any insect to synchronously complete diapause development.

That fall I divided the collection into four lots by weight and deployed two of them in much colder sites than Berkeley, the inland Contra Costa shed and Blodgett Forest at 1450-m elevation in the Sierra Nevada. One lot was retained in the cage at Berkeley and one indoors (20±2 °C). The results were as expected; during 19 days in May 1986, 61 *P. y-inversus* emerged from the Blodgett and Contra Costa winters, none at Berkeley.

During that era, insect/plant biologists were fond of the term "strategy" to describe genetic and evolutionary adaptations, such as development of chemical defenses by plants to deter insect feeding, as though the adaptation was purposeful, rather than by natural selection. The term had been used to explain diapause holdover when most larvae developed following the first winter, then successively fewer in the succeeding several years, which sometimes happens when larvae or pupae are reared and held over winter indoors. I believed that for *Prodoxus*, the temperature over winter was the primary factor in development on an annual basis, rather than a prescribed genetic sequence.

Therefore, with numerous *Prodoxus* at hand still in diapause, I decided to test the "strategy" hypothesis. I deployed the yucca fruit remnants to an unheated mobile lab temperature for two winters (November 1986–March 1988) and again in fall 1988. The 20th-year class proved to be the largest, with 74 *P. y-inversus* emerging in April 26–May 8, 1989, after winter at Blodgett, and 77 in April 12–23 at Berkeley; the total (151) was 29 % of the ultimate total emergence. I repeated the test more convincingly by holding the remaining larvae at constant temperature for 4 years (1990/1994), then at cold winter sites (Blodgett and Big Pine, Inyo Co.). The 25th-year class in 1995 comprised 125 *P. y-inversus*, 24 % of the total emergence. Finally, after another 4 years of constant 70 °F, X-rays of several pods prior to the 30th year revealed no remaining viable larvae. However, another four winters at constant 70° and exposure to California winters resulted in emergence of 14 individuals in 1999, from April 26 to May 26, 30 years following their feeding and cocoon construction.

The ability to sense conditions and to survive long-term diapause could be termed a "strategy," but the timing of diapause development and completing metamorphosis are determined by outside factors, particularly temperature, at least in *Prodoxus*. Maturation sometimes occurs in response to temperatures that in earlier years did not elicit development. There was virtually no response to my report of the longest insect dormancy and synchronized, seasonally timed emergence, leading me to wonder if a lot of entomologists did not believe it.

Life History I was incredibly fortunate to have been raised by parents who valued education, born too late to have seen Armed Service duty in WWII; to have been eligible for student deferments through the Korean conflict; and was too old for Vietnam. I entered University of California, Berkeley, after 2 years at San Diego State College (which avoided ROTC required of freshmen and sophomores at Berkeley). I was so naive that I did not even know there was a field called systematics or that people could actually make a living doing museum work. Moreover, my years in graduate school spanned a time of accelerated expansion in academia with the return of Korea veterans and increased government support for the sciences, with NIH and NSF funding that followed the Russian Sputnik success. As a result, I was able to assume a position in the Agriculture Experiment Station at Berkeley that could not have suited me better had I been asked to write the job description. I was half-time with the California Insect Survey (CIS), a federally funded project, and half-time for research. Our survey efforts were given direction by perceived geographic gaps in collection records in California and by taxonomic interests of specialists, many of whom were interested in doing regional surveys through the first three decades of the CIS Bulletin.

Overall, my penchant for collecting, for the California Insect Survey, for systematics research, and for larval discoveries have provided a rewarding life full of unending discoveries.

The Future? People of my generation, born in the 1930–1950s, have witnessed massive changes in society, surviving (or not) four wars, each more futile than the one before, and we have seen rapid changes in all walks of life. Xerox replaced carbon copies (but not before I had to produce four copies of my thesis), then PCs replaced electric typewriters, and we saved copies of a thousand messages, manuscript starts, and multiple flash drives. Film cameras became obsolete overnight, and countless past images were digitized and stored in places we can't remember. Books and journals in libraries are being replaced by online copies to an extent that today's students feel no need to search further than their desktop PC, and assume that if they can't find it online probably it is not important. Building a professional library to carry to another institution used to take a lot of our time as PhD students. Now it is just Google and a laptop. Local independent book stores and their personnel fell victim, along with printing and jobs in many other fields. Emphasis on molecular traits has essentially replaced morphological structures and therefore professional phylogenetic and systematic analyses will be restricted to those having access to costly molecular labs and to publication costs to make their studies available.

A truly disturbing trend has been replacement of general collecting to few target taxa. Permits often are required and complicate general collecting, which is also discouraged by deeply misguided folks who believe normal collecting affects insect populations. Small mammal and bird pairs may produce 2 or 4 eggs, then spend the rest of the season caring for their offspring, whereas any given female moth may deposit 200 or 400 eggs, then leaves them and the resulting larvae to fend for themselves. On average, in order to maintain a stable population all of her hundreds of offspring except two must die before transformation to the next generation. There is no evidence to validate the notion that normal collecting has any lasting effect on insect populations; loss of habitat to human activities is their primary enemy. Applying the same criteria to insects that are used to define endangered species of vertebrates is absurd.

As transportation improved following WWII, more people visited more remote places more often to collect, but it appears to me almost all have become specialized collectors. As young systematists we routinely collected a diversity of insects, for colleague friends or for taxonomists of the future (including ourselves), aware that a high percent of the effort was duplication. By contrast, in recent decades the focus of field trips often is a single species, genus, or family, handled for molecular use, and, no specimens are collected as byproducts for use by future colleagues. It can be argued that general collecting is inefficient duplication. However, spending the time and money to plan and visit distant places and collecting only target species is even more inefficient. I recall John Chemsak predicting this shift more than 40 years ago, even before the molecular revolution in systematics: "students will say oh, yeah, those old guys used to collect all kinds of insects (ha, ha)." I scoffed; but he was right. In addition to hundreds of other new species we discovered, he and I have had >80 patronyms named in our honor, species representing seven insect orders, testament to our inefficient efforts. That just is not likely going to happen again.

References

Brown JW, Powell JA (2000) Systematics of *Anopina* Obraztsov (Lepidoptera, Tortricidae, Euliini), vol 120. University of California Press, Oakland, 128 pp

Powell JA (1973) A systematic monograph of New World ethmiid moths (Lepidoptera: Gelechioidea). Issue 120 of Smithsonian contributions to zoology. Smithsonian Institution Press, 302 pp

Powell JA (1976) A remarkable new genus of brachypterous moth from coastal sand dunes in California (Lepidoptera: Gelechioidea, Scythrididae). Ann Entomol Soc Am 69:325–339

Powell JA (1991) A review of *Lithariapteryx*, with description of an elegant new species from coastal sand dunes in California. J Lepid Soc 454:89

Powell JA (2001) Longest insect dormancy: yucca moth larvae (Lepidoptera: Prodoxidae) metamorphose after 20, 25, and 30 years in diapause. Ann Entomol Soc Am 94:677–680

Powell JA, Ferguson DC (1994) A new genus of winter moths (Geometridae) from eastern California and western Nevada. J Lepid Soc 48(1):8–23

Powell JA, Opler PA (2009) Moths of Western North America. University of California Press, Berkeley, 569 p + 1200 color images

Prof. Jerry A. Powell is an emeritus professor at the University of California, Berkeley. An incurable collector from an early age, he took up his lifelong hunt for moths and butterflies at the age of 13, influenced by a summer nature study course offered by Charles Harbison at the San Diego Museum of Natural History. Jerry's undergraduate study, San Diego State College and University of California, Berkeley, was followed by graduate study at Berkeley leading to PhD in 1961. Influenced by H. H. Keifer in Sacramento, and encouraged by R. M. Bohart at Davis and Berkeley faculty, he undertook study of systematics and larval biology of microlepidoptera. There were no active microlep specialists in western North America, and Tortricidae seemed to be a fruitful starting point, having numerous species of importance in agriculture and forestry. An appointment in the Agricultural Experiment Station at Berkeley led to a diverse array of studies, systematics of ethmiid moths, fungus feeding microleps, biosystematic and pheromone relationships among conifer feeding *Choristoneura*, long-term diapause in yucca moths, and oviposition patterns among Australian Tortricinae. He made numerous trips to Mexico and Costa Rica in quest of tortricids and other microleps. He taught the department required summer field course in the 1960s, Systematic Entomology, Immature Insects, and co-taught basic entomology in later years. NSF and US Forest Service supported research during the 1960–1980s, and a PEET enabling grant produced fine studies by numerous graduate students. Jerry served as acting editor of *Pan-Pacific Entomologist* (1959–1960), and President (1964); *Journal of the Lepidopterists' Society* and its supplement series (1964–1972) and President (1988); Panel of Advisory Editors UC Publications in Entomology and the Bulletin of the California Insect Survey (1963–1987); Society of Systematic Zoology, President (1989); and Board of Editors, *The Moths of America North of Mexico,* 1979. He has published about 240 journal papers, monographs, books, and web-posted database reports. Honors include Fellow, California Academy of Sciences (1971); Karl Jordan Medal, The Lepidopterists' Society (1982); The Berkeley Citation, University of California, Berkeley (2000). In retirement, he has been conducting long-term inventories of Lepidoptera at Berkeley, California Channel Islands, and several UC Natural Reserves.

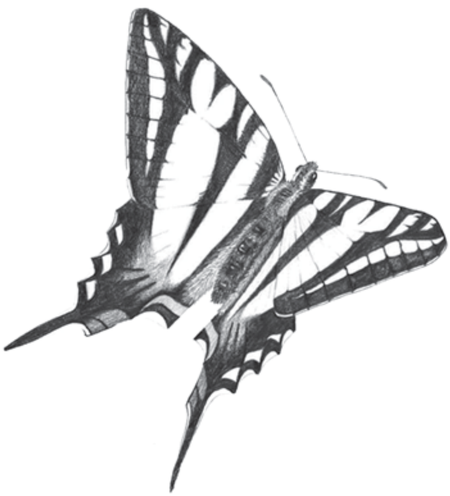
Part V
Secret Lives of Lepidopterists

Each of us carried a compass and a spirit flask, necessary appendages of the cautious pioneer.

Samuel H. Scudder, lepidopterist and first Vice President of the Appalachian Mountain Club (AMC), from his account in *Appalachia* on the first ascent of Mount Adams (New Hampshire, USA).

In 1876, Samuel H. Scudder, a prolific lepidopterist from the USA, was one of 34 founding members of the AMC, which is the oldest mountaineering and conservation club in the USA, and the first editor of the AMC journal *Appalachia*. His mountaineering feats are a less-known part of his life—most lepidopterists might know him better as the first editor of the esteemed journal *Science*. Scientists are typically portrayed as one-dimensional, geeky, and uninteresting, but it is the “secrets” about their lives that make them multidimensional—from a beautiful tradition of passing on brandy glasses, to eating pan-fried grasshoppers during the rice harvest in South Korea, to colorful conversations with the border patrol.

LAD



Neographum marcellus. Illustration by Brianne Boan, from photo with permission by Bryan E. Reynolds

Chapter 14
A Tale of Two…Glasses?

John Brown

It was the best of wines, it was the worst of wines … port wine, that is. But I'm getting way, way ahead of myself. So let me start again….

I consider myself a microlepidopterist—not a tiny person who studies moths, but a normal-sized person who studies tiny moths. Although we may boast a long legacy of champions—Linnaeus was actually the first person to describe a microlepidopteran—I really do not think of us as having many of your standard time-honored traditions … but of course, I could be wrong (duh!). Like most scientists, we enjoy bashing, or at least augmenting, modifying, or fine-tuning the hypotheses, concepts, and methods of those who came before us—nothing is sacred. Our science, like all science, moves forward by questioning the findings of our predecessors, mentors, and peers. Furthermore, in the constant barrage of technological advances, there are fewer and fewer systematic and traditional methods that we have in common with those who laid the foundations of our science. For example, Edward Meyrick (1854–1938), the "godfather" of microlepidoptera who described over 14,000 species of little moths, relied exclusively on superficial characters of the wings and body. His descriptions of new species were concise and accurate, but woefully incomplete by today's standards. Nonetheless, as a teacher of "the classics," each and every one of the Latin names (all species must have a scientific or Latin name) proposed by Meyrick is exceptional in its Latin derivation and grammatical structure. The closest some of us cretins come to Latin today is pig-Latin. The study of Latin? Now, there's a long lost tradition.

In the 1920s, the British pair of F. Pierce and J. Metcalfe began exploring the concealed anatomy of the male and female genitalia through careful dissection of the abdomen of adult moths. It was not long before these structures became the primary character for differentiating species, and their use in descriptions of new species became standard and essential. We still rely on these characters but perhaps

J. Brown (✉)
Smithsonian Institution, Washington, DC, USA
e-mail: tortricidae.jwb@gmail.com

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_14

not with the same zeal. Later came scanning electron microscopy (SEM)—probably most skillfully embraced by Don Davis (National Museum of Natural History)—which dug deeper and deeper into morphological features barely discernible using dissecting and compound microscopes. Although SEMs were not employed by the masses, owing to the inaccessibility of electron microscopes to many workers, Davis and others discovered many morphological features of considerable value in deciphering the relationships among families and other groups of mostly primitive moths. As for SEMs, well, I do not see them much in the Lepidoptera papers anymore (although I recently included a pair in a paper).

By the mid-1980s, the use of computer-assisted methods for crunching data to build the much sought phylogeny of groups (trees or diagrams which portray genealogical relationships) were in full swing, with highly contentious arguments regarding which algorithms or mathematical models best revealed the "true" (HA!) phylogeny of any given group. During this period, those who organized groups by phenetic methods (based on overall similarity) were replaced by the cladists (Hennigian phylogeneticists) who organized groups based on shared advanced characters. Computers have not gone away … yet.

By about 2010, even the most traditional systematists (i.e., oldest, or more diplomatically, most senior) had seen the molecular light and were embracing the use of at least one gene (the mitochondrial gene cytochrome oxidase I—a.k.a. the "barcode of life") to differentiate taxa and/or identify relationships. There is nothing like a big ol' neighbor-joining tree ("neighbor-joining" referring to the mathematical algorithm that links or clusters the DNA sequences by similarity) to keep a systematist entertained for hours! That's not to say that the previous, traditional methods were abandoned with each advancement—many merely took a backseat as the new methods were incorporated into a growing toolbox of systematic techniques.

To be perfectly honest, there are many things that I do today the very same way I learned to do them in graduate school back in the 1980s. But that's not to say I do them for traditional reasons. I suspect I do them mostly because I am just too lazy to change. For example, I learned to make microscope slides of the genitalia using Canada balsam as the mounting medium. Today, a material called euparol is the medium of choice—it makes clearer slides that potentially last longer without yellowing—but I just cannot seem to change … too old and set in my ways, I guess. I also do other things in a rather old-fashioned manner; I frequently use blocks (something you might find in an old curiosity shop) rather than spreading boards to set specimens. Hmmm. But some of this can be explained by personal preference, simple resistance to change, or plain laziness in my case, rather than "tradition." However, in contrast to my turn-of-the-century predecessors, I use a battery-powered ultraviolet light (blacklight) and a plastic bucket trap with a light-weight aluminum funnel and plexiglass baffles rather than a Coleman lantern and a bed sheet to attract moths at night; I use plastic Nalgene vials and 100 % alcohol in a freezer kept at − 80 °C to preserve specimens for molecular analyses; and I set (= pin and spread) my microlepidoptera in small plastic boxes with dense plastozote foam. Hence, in regard to methods and techniques, even though I may be old fashioned, there are exceedingly few things I do that can be considered "traditional."

So how about Lepidoptera traditions from a social perspective? Although I consider myself a rather gregarious sort, I am at loss to come up with many traditional social aspects of lepidopterists … although I can think of a stupid one. At the annual meeting of the Lepidopterists' Society, the incoming president receives, from the outgoing president, a headband that bears a pair of styrofoam antennae at the end of pipe cleaners; and he is obliged to wear these antennae for the remainder of the business meeting. Now there is a fine tradition.

So now that I have convinced you, or at least myself, that there are a few traditions in the Lepidoptera world, let me tell you about a tradition known only to a handful of microlepidopterists, a tradition of which I became aware just a few years ago….

My story begins with Thomas de Grey, sixth Baron Walsingham (1843–1919; known simply as "Walsingham" to most microlepidopterists), who was born in London and educated at Eton and Trinity College in Cambridge. Lord de Grey sat as a Conservative member of the British Parliament from 1865 until 1870 when he succeeded his father and entered the House of Lords. In stark contrast to his political obligations, Walsingham was an avid lepidopterist and collector, primarily of microlepidoptera, an avocational interest that developed at an early age. His collection (estimated at over 260,000 specimens), which was eventually sold to the British Museum (now The Natural History Museum, London), was among the most important ever assembled. For many of us, Walsingham is to microlepidoptera systematics what Darwin is to evolutionary theory. His impressive published works and massive collection represent an invaluable cornerstone of the foundation upon which the modern systematics of many microlepidopteran families is based.

When Godman and Salvin embarked on their grandiose project near the turn of the nineteenth century, a series of volumes titled *Biologia Centrali-Americana,* Walsingham was drafted to write the volume on microlepidoptera (Volume IV, Lepidoptera-Heterocera, published 1909–1915). Early in the process, Walsingham enlisted the assistance of August Busck (1870–1944), a Danish-born American entomologist who worked for the U.S. Department of Agriculture (USDA) at the National Museum of Natural History (USNM), Smithsonian Institution in Washington, D. C. Busck's expertise included many microlepidoptera groups, especially those in the New World tropics; he had spent a considerable amount of time collecting in Panama, prior to the construction of the canal, investigating mosquitoes as vectors of diseases. Busck was a careful worker with an exceptional publication record, and he was revered and respected by colleagues and students, alike. He was largely responsible for the tremendous growth of the microlepidoptera collection at the USNM through fieldwork and acquisitions of major collections. In 1908, Busck was invited to England to help his friend and colleague, Lord Walsingham, with the *Biologia* volume treating the microlepidoptera of Central America. Among the things that Busck brought back with him upon his return to America was a pair of small, handsome port wine glasses etched with the Walsingham crest, which Lord de Grey had given him as a symbol of friendship and gratitude (Fig. 14.1).

Fig. 14.1 The Walsingham glasses given to August Busck

In the late 1930s, as Busck's career was winding down, the torch was passed to young John Frederick Gates Clarke (1906–1990) ("Jack" to his friends and colleagues) who came onboard the USDA at the USNM. Originally working on macrolepidoptera (the larger moths), upon the retirement of August Busck in 1940, Jack switched to microlepidoptera, following in Busck's footsteps, making his greatest contributions to the study of these small moths, and like Busck, primarily the superfamilies Gelechioidea and Tortricoidea. Jack's highly productive career at the USNM (1936–1975) spanned that great transition from the early American, turn-of-the-century lepidopterists (e.g., Schaus, Dyar, Busck, Heinrich, et al.) to the modern, or at least current, lepidopterists that occupy offices at that institution today; that is, Don Davis, John Burns, Robert Robbins, Alma Solis, Mike Pogue, and I, all overlapped with Clarke to some extent (the youngest of us as postdocs after Clarke's retirement). As a driving force behind the creation of an Entomology Department separate from the Department of Zoology at the Smithsonian, and as its first chairman (Jack jumped ship from the USDA to the Smithsonian in 1953), Jack had a significant and lasting impact on the collections, the staff, and the overall success, notoriety, and productivity of the department.

Immediately before coming to the museum, Jack had begun work on his PhD at Cornell University, which he left in 1936 to take a position with the USDA, enticed by the highly lucrative salary—$3200/year! Jack was stationed at the museum most of his career, but served in the Army in Europe during World War II. After the War he was detailed to the British Museum (Natural History) to compile a series of catalogs on the types of microlepidoptera in that museum described by Edward Meyrick. The result was an impressive eight-volume set that provided for the first-time images of adults and genitalia of these types (the unique specimen upon which the concept of a species is based) to the world community of lepidopterists. For that work, he received a PhD from the University of London in 1949. Before the War, Jack worked closely with Busck, and near the end of Busck's career, he passed to

Fig. 14.2 Tortricidae in the USNM collection *(Left)*. Lepidoptera on spreading blocks *(Right)*

Jack the handsome pair of port glasses that Busck had received from Walsingham. The glasses were among Jack's prized possessions.

Jack was a skilled field biologist and an active member of a local group called the Washington Biologists' Field Club, serving as its vice president in 1984–1985. He also was known for his culinary skills, and particularly for his potatoes with a "small dash" of whiskey that were served at the club's events on Plummers Island. The club was organized around the turn of the century (ca. 1901), and August Busck, an avid field biologist and collector himself, was one of its early members, elected to membership in 1903. Hundreds of specimens of microlepidoptera collected by Busck on Plummers Island (ca. 1901–1910), the club's "research station," are deposited in the collection of the USNM (Fig. 14.2). One of the long-term goals of the club was to compile an inventory of the biota of the island, and both Busck and Clarke contributed to this end. In Jack Clarke's oral history, he recalled that Busck left the club early on (ca. 1910) when the club unjustifiably raised its annual dues from $2 to a whopping $3, obviously too steep for Busck.

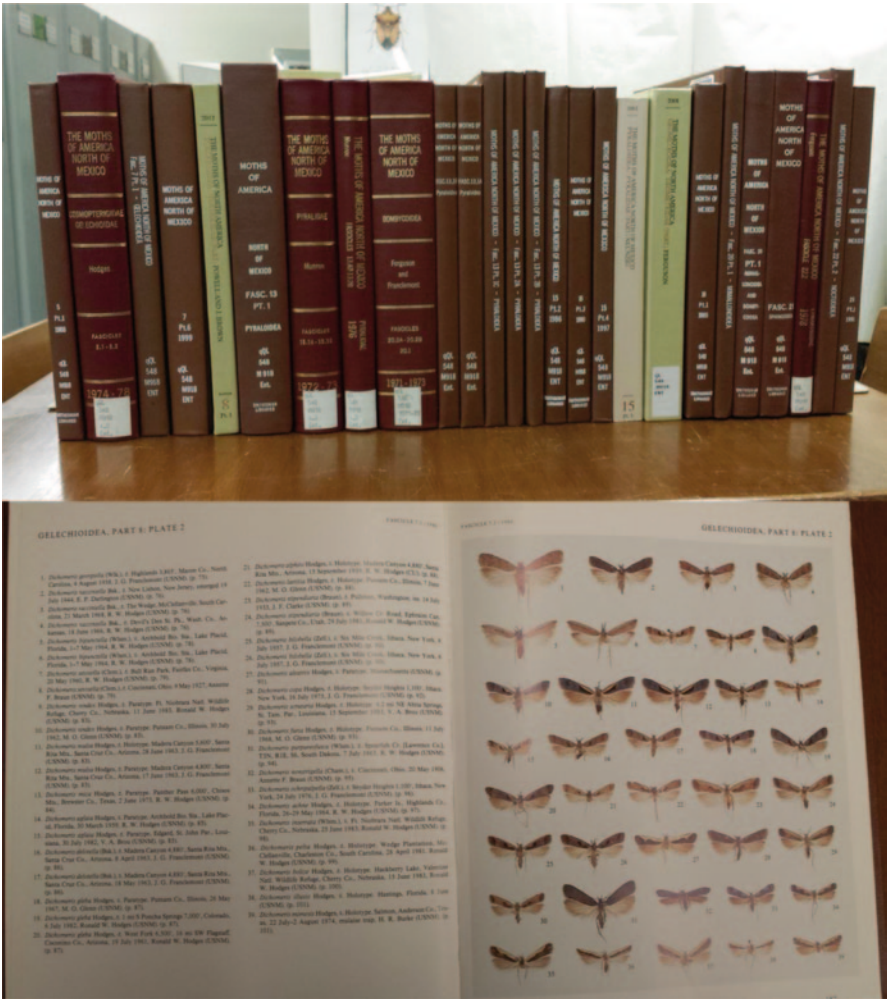


Fig. 14.3 Fascicles published by the Wedge Entomological Research Foundation *(top)*, with a page of illustrations from a Gelechiidae fascicle *(bottom)*

In the early 1960s, the long legacy of Cornell students in the USDA's Lepidoptera unit who had been trained by Jack Franclemont began at the USNM with the hiring of Ron Hodges. For many decades thereafter, virtually all of the moth taxonomists/curators at the National Museum (i.e., Donald Davis, Ronald Hodges, Douglas Ferguson, Robert Poole, and postdocs such as Richard Brown) were students who earned their PhDs at Cornell under the guidance of Franclemont. Ron's forte was the microlepidopteran superfamily Gelechioidea, a group whose systematics was pioneered by Busck and subsequently studied extensively by Clarke. Like Busck and Clarke before him, Hodges was also an enthusiastic field biologist. He also was an excellent curator, a prolific publisher of scientific papers, and a superb preparator of microlepidoptera specimens (reflecting his training from Franclemont).

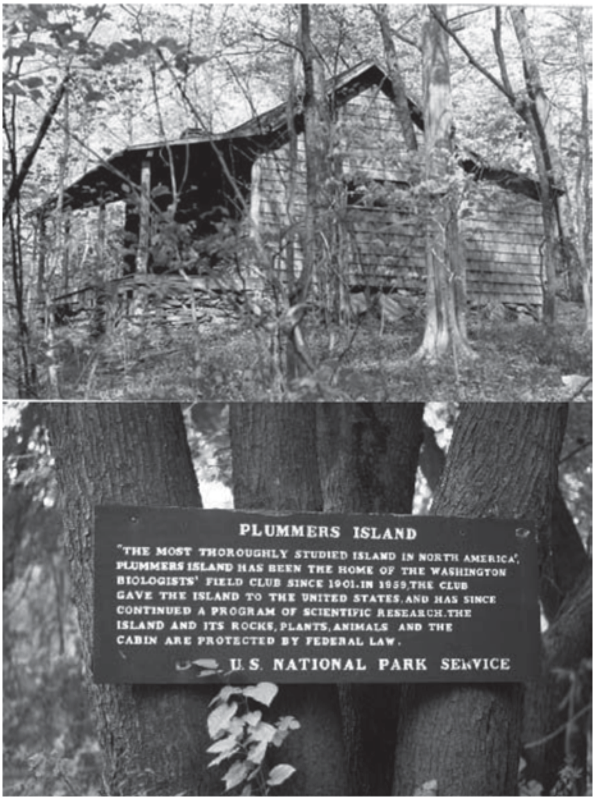


Fig. 14.4 Historic cabin at the high point on Plummers Island *(top)*, and sign at entry point to the island *(bottom)*

Specimens collected and prepared by Franclemont and Hodges are immaculate, easily recognized in the USNM collection, and hence, frequently used for illustrations in scientific publications. Ron was an active member of the Washington Biologists' Field Club, serving as president (1976–1979) and as "cook" during the biannual outings on Plummers Island (Fig. 14.4), inheriting this chore from Clarke. Ron and his wife Elaine (a noted scientific illustrator at the National Museum) were participants in many museum activities and were fixtures at all Entomology Department functions. With Clarke's retirement, the microlepidoptera torch passed to Hodges, and so did the Walsingham glasses.

Ron was extraordinarily farsighted in regard to the future of Lepidoptera research on the North American fauna, and in collaboration with several colleagues, founded the Wedge Entomological Research Foundation (in the late 1960s) with a substantial endowment from the Dominick family. The flagship publication of the foundation, a series of fascicles called *The Moths of North America* (a.k.a. *MONA*) (Fig. 14.3), became the premiere vehicle for the publication of systematic monographs on the fauna of North America (north of Mexico). Ron contributed fascicles on Sphingidae, Cosmopterigidae, Oecophoridae, and Gelechiidae (one on Dichomerinae and one on the genus *Chionodes*), and for these contributions he received the

Lepidopterists' Society's prestigious Karl Jordan Medal in 1997. After a remarkably productive career of over 35 years with the USDA's Systematic Entomology Laboratory (SEL) at the Smithsonian, Ron retired in 1997.

In January of that year, I joined the staff of SEL as Ron's replacement—truly a dream come true for me. I was a late bloomer and had been unable to find a position in systematics after earning my PhD at the University of California, Berkeley (1988), followed by a postdoctoral position at the Smithsonian Institution, and a technician position at the Los Angeles County Museum of Natural History. I was working as an environmental consultant in San Diego, California when I received the call from Ron asking me if I would be interested in applying for the position. I was 45 years old when I started with SEL, but despite my age I was the proverbial kid in a candy store. To come to work every day to the Smithsonian, to play in the enormous moth collection at the National Museum, and to share my scientific findings via published papers was absolutely unbelievable. I suspect I appreciated the position more than most because I had spent a considerable amount of time in private industry in a job that was not particularly fulfilling, and I had always dreamed of a position in research, but had abandoned that dream.

The focus of my research was and still is the family Tortricidae (known as leafrollers); I concentrated on those groups of interest to American agriculture—pests, invasive species, biological control agents, etc. Unaware of the "traditions" of my predecessors, I accepted an invitation to join the Washington Biologists' Field Club in 2000, serving as its president in 2008–2011. I spearheaded the publication of an inventory of the invertebrates of Plummers Island (2008), and I remain active in the club's activities. Like my predecessors, I have a passion for fieldwork, participating in faunal inventories in Costa Rica, Miramar Air Station in San Diego, the Great Smoky Mountains National Park, and elsewhere. I also have indulged in many "bioblitzes," and I am an enthusiastic backyard collector of all families of Lepidoptera, but of course, mostly microlepidoptera.

In 1998, I was invited to become a board member of the Wedge Entomological Research Foundation, a position I graciously accepted. In recent years (since about 2007), my wife Poody and I have hosted an informal dinner following the annual meeting of the board. And in 2009, I became a part of a little-known prestigious (to me) microlepidoptera tradition. Ron secretly brought the Walsingham glasses to the dinner (with the assistance of John Burns), along with a bottle of very fine, old port wine. And as the evening wound down, Ron introduced me to those handsome little glasses, told me about their long tradition, and gave them to me. We toasted Walsingham, Busck, and Clarke with the fine port wine, which was aged and thick; it had to be strained with cheesecloth before drinking. And although I certainly did not recognize its quality (I am no wine aficionado), I savored each sip. It was undoubtedly the most memorable occasion of my entomological career, and it was highlighted by the fact that it was shared with several of my closest colleagues and best friends. Although it is unlikely that I will ever be in the same league as my predecessors, I am hoping that I have at least one more decade to continue to add to my lepidopterological accomplishments.

Few things in my life have given me the feeling of being a part of something big, something special, a sense of continuity with the past, and the feeling of passion, camaraderie, and discovery that I have experienced working on the systematics of microlepidoptera for the USDA at the National Museum of Natural History, belonging to the Washington Biologists' Field Club, serving on the Board of the Wedge Entomological Research Foundation, and possessing, even if only temporarily, the Walsingham glasses.

With my retirement this year, I grow eager to see to whom the Walsingham glasses may pass in the future. I anticipate that the USDA will hire a young microlepidopterist to replace me, and I have great expectations that he or she will have a passion for collections, descriptive taxonomy, and fieldwork shared by the former microlepidopterists who have occupied the USDA position at the Smithsonian Institution.

John Brown is a retired research entomologist. He received his bachelor's degree from San Diego State University and his PhD from the University of California, Berkeley. He has spent the past 17 years of his career with the U.S. Department of Agriculture's (USDA) Systematic Entomology Laboratory (SEL) at the National Museum of Natural History, Smithsonian Institution in Washington, DC. He has a passion for the systematics and diversity of Tortricidae, and he continues to work on the Smithsonian collection and conduct research on these ugly little brown moths. He has published over 170 research papers, notes, book chapters, and monographic treatments on Lepidoptera, and has served as the president of the Lepidopterists' Society, the Entomological Society of Washington, the American Association for Zoological Nomenclature, and the Washington Biologists' Field Club. He enjoys collecting moths, participating in Lepidoptera courses, and vacationing with his wife, kids, and grandkids.

Chapter 15
Journeys of a Microlepidopterist—from South Korea to Arizona

Sangmi Lee

The sun is setting in the west, and it's getting dark. I just finished hanging a white sheet on a rope between two trees, as well as ultraviolet (UV) and mercury vapor lights. Now, I am seated on a folding chair and sipping a can of beer, looking at the sheet to see if any insects fly to my lights. Finally, insects are slowly coming to the lights and preparing to land on or crawl around the sheet. This is their party time today. If the weather, including factors such as wind, humidity, and temperature, is perfect for insects flying, a plethora of insects will show up at different times throughout the night, all the way up to sunrise.

It's now almost the middle of the night. All my vials are filled with a single micromoth in each one, and the dumping jars are filled with macromoths. It is now time to pack my light-collecting gear and get back to the cabin where I will stay for the night. There is a big smile on my face as I am driving back. As soon as I get to the cabin, I put the vials of moths in a ziplock bag with a label that includes locality information and place them into the freezer to kill them.

The next morning while I brew coffee, I gather my mounting gear, including the squares of plastozote foam in which I've cut narrow grooves with a razor, micropins (also called minutens), and forceps with curved sharp points. Spreading the wings of these micromoths is essential to see the wing patterns used to identify species, and this has to be done as soon as possible before they become too dry. Pinning moths is one of the activities that I thoroughly enjoy and am especially skilled at doing. Here I will share my technique of how I mount micromoths. After removing the vials of specimens from the freezer, I select a specimen with forceps and place it in the groove between my thumb and finger. Then I use my forceps to select a 0.20 (mm diameter) minuten, which I insert into the center of its thorax. For very small micromoths, I may use a 0.15 minuten. Holding the top of the minuten with the specimen, I softly blow on the wings of the moths from their underside to be loosened. The specimen is placed in the groove of the foam, the curved tip forceps

S. Lee (✉)
Arizona State University, Tempe, USA
e-mail: slee281@asu.edu

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_15

Fig. 15.1 Sangmi pinning micromoths in the field, La Purico in Mexico

are used to lift the wings into a spread condition. The wings are then covered by wax paper, and the position of antennae and legs are adjusted (Figs. 15.1 and 15.2). Mastering this skill requires both practice and perseverance. After destroying scores of specimens in practice, I am now capable of mounting one specimen in less than 2 min; my method is demonstrated on youtube.com in a video entitled *Collecting and Pinning Microlepidoptera*.

Fig. 15.2 Micromoths pinned on a Styrofoam by Sangmi

In my first year in the USA, after coming from South Korea, I had an opportunity to participate in a Bioblitz of Lepidoptera in the Great Smoky Mountains National Park for an all-terrestrial biota survey. As soon as I arrived at the station where participants gathered together for night collecting, my heart began to beat rapidly because Dr. Ron Hodges, a world-renowned expert on North American gelechiids, was walking towards me for our first meeting. After introductions, we packed for the first night of collecting. When we reached our collecting spot, the bedsheets were pinned to a rope between the trees, and a 15-W UV light was suspended in front of each sheet. After the lights were connected to the batteries, we began walking around each sheet, one at a time, searching for the first moth that would appear. During our visits from one light to another, Dr. Hodges encouraged me to turn off my headlight and enjoy the stars and the sounds of Mother Nature in the woods around us. In this one night, I learned a lot from him about the gelechiid species in the Smoky Mountains, how to collect them and also how to enjoy a night in the woods.

One of my favorite experiences in the field was participating in the Arthropods of La Selva (ALAS) project by making an expedition to Finca Murillo in Costa Rica in April 2005. My colleague, Sibyl Bucheli, and I were picked up at the San Jose airport and taken directly to the La Selva Biological Station. The rough and curvy road was more than my stomach could handle while riding in the back of the field truck. As a non-Spanish speaker, my hand signals and body language to the driver about needing to stop must have worked, as he pulled over to give my queasy stomach a break. When we arrived at the station, the kitchen was closed to two ladies desperate for food. The next morning about 15 people, including other participants and local people, gathered at the station for the hike to a small farm adjacent to Braulio Carrillo National Park at about 1500-m elevation (Fig. 15.3). The local people were hired to carry our gear and food, which was a great relief. I have to admit that I'm not a big fan of hiking. Most of the others reached the farm in less than 5 h, but I was almost an hour behind them.

Fig. 15.3 Murillo house on ridge tops and shallow slopes in a mosaic cleared pastures and mature forest. (Photo by John T. (Jack) Longino at the University of Utah)

Fig. 15.4 Sangmi collecting moths at night with mercury vapor light in Costa Rica

While staying in the farm, the mercury vapor light was used with the UV light to collect arthropods at every night. Macromoths and beetles are known to be more attracted into the mercury vapor light than the UV light. It is so easy to me to eat lots of insect protein while collecting moths at the mercury vapor light. It happens a lot more to me while I have company because my mouth opens frequently without thinking (Fig. 15.4).

For the first time in my life, I experienced 14 days without hot water and electricity, along with typical amenities like a refrigerator and freezer for killing the moths that I collected. We used a generator to operate a mercury vapor lamp for collecting, and the sheet was covered every night with a huge number of moths, even when the rain poured heavily on some nights. My daily routine was typical of other field trips, beginning with a cup of coffee following by pinning and spreading moths the rest of the day. My shower time changed to noon when the sun was high and the temperature was suitable for my body to resist the cold water.

I grew up in South Korea, spending my afternoons playing soccer with boys until the time for fall rice harvest arrived. Before the harvests began, grasshoppers would appear in the fields, and I would chase and capture them in the early morning. I would carry a container full of grasshoppers home, where my mother panfried them for me, and I would eat their legs (Fig. 15.5). I still remember that they tasted like crunchy potato chips. I think it was at this time that my love for catching insects was born.

My fascination with insects led me to concentrate on entomology during my undergraduate program at Kangwon National University in South Korea. I enjoyed being a college student but wasn't really searching for a career. However, I had the opportunity to work as a student volunteer in a lab that was focusing on biological control of insect pests. My main task involved getting chicken livers from local farmers and using them to help graduate students formulate an artificial diet to raise beetles or moths. During a training event for all students working in insect labs, I was introduced to insect collecting. I was not interested in daytime activities because I preferred to stay inside, especially during the hot summer season; however, lab members began setting up night collecting lights above a sheet stretched

Fig. 15.5 Edible grasshoppers fried in an oil pan. (Photo by Seungho Kang in South Korea)

between two poles. Most lab members were focused on capturing the large insects, but there were lots of small things flying around that I couldn't resist trying to catch. I finally caught one in a glass vial, and it was a beautiful and peculiar micromoth with scales flattened on its head; shiny fringe hairs on its wings; long, thin antennae; and long hind legs with hair brushes. Before I knew it, my pockets and hands were filled with vials of captured micromoths. This night of collecting is what sparked my interest in microlepidoptera.

As a graduate student at Kangwon National University in Korea, I spent nearly 16 h a day, 7 days a week at school, except on major holidays such as Thanksgiving or New Year's Day. This was a typical occurrence in Korea, and Asia in general, because graduate students were expected to arrive at the school before their professors and to stay later than their professors as well. I usually stayed in the lab from 8:00 a.m. until 11:00 p.m. or midnight, and sometimes I even stayed overnight in the lab. I took four courses during my first two semesters, two courses during my third, and one course during my fourth semester. The coursework wasn't difficult compared to that of the US system but the expectations were higher for us. In my lab, the majority of our time was spent completing our own projects and helping others with theirs and learning from the seniors. During my first year in the graduate program, there were only eight graduate students in Dr. Park's lab, but we increased to 12 during my second. We spent all of our time together as though we were a family of entomologists. Having females in any entomology lab was atypical, but this was especially so for labs focusing on insect taxonomy. Two reasons out of many that women don't often seek taxonomic work are that much of the work is done in the field and not many women are attracted to careers in taxonomy. Our lab didn't have any female workers for quite some time. All of that changed when a female student entered our lab just 1 year ahead of myself. As a result, there weren't any exceptions for me as a female. While in the field during collecting trips or while attending conferences and meetings, we always shared rooms and work was shared equally among everyone—including carrying the heavy generator.

Every lab has its own management system. In our lab, we were like soldiers with our very own titles and with a kind of ranking system. As graduate students, we mostly were trained by and learned from our seniors. First year doctoral degree candidates instructed second year master's degree students, and the second year master's degree students taught the first year master's students. The lab meeting was held weekly and led by one of the higher-ranking people, and our advisor led a monthly meeting. Each year our lab had at least ten ongoing projects, and more than half of these projects were for surveying the fauna, especially moths. After the specimens were collected in the field, they were brought into the lab. Then, our lab members would mount all of the specimens over the next 2 or 3 days. During these 2 years of my life, I spent every summer pinning thousands of moths, from micros to macros. As a graduate student of Dr. Kyu-Tek Park, I received my Master of Science degree with my thesis entitled *Systematics of Subfamily Gelechiinae in Korea*.

In 2007, I completed my PhD under Dr. Richard L. Brown with my dissertation entitled *Systematics of Holarctic genera of Teleiodini* (Lepidoptera: Gelechiidae). Now, the tribe Teleiodini is a junior synonym of Litini. This was the first phylogenetic study of a group of Gelechiidae that employed both molecular and molecular data. I have to say I was incredibly lucky to work with Richard Brown as my doctoral and postdoctoral adviser, who I call both a mentor and a friend. Mississippi Entomological Museum is the second largest university collection of Gelechiidae in the USA and is surpassed only by the University of California, Berkeley. After almost 10 years of being in Mississippi, I learned and developed new techniques while studying the morphology of moths. Richard had devised a technique for descaling whole bodies of moths and slide mounting the parts to prepare whole body mounts. I used his method that allowed examination of many new anatomical characters besides the traditional limited set of characters that emphasized scaled appendages, venation, and genitalia, although I did incorporate wing venation into my mounts. With this method, I remove the left pair of wings and dry-mount them under a coverslip glued to the slide, and then the right wings are descaled and stained and then mounted in euparol on the same slide to show their venation The rest of the specimen is disarticulated to separate the head, antennae, prothorax, mesothorax, metathorax, genitalia, and abdomen and then mounted on a second slide also (Fig. 15.6). The new morphological characters are revealed after comparing slides from different specimens under the microscope.

Each year that I was pursuing my PhD followed by my postdoc in the museum, there were many trips for collecting, and sometimes these were combined with attending professional meetings. I was the only student of Richard's studying Lepidoptera until Edda Martinez arrived from Puerto Rico, and after she graduated, David Plotkin joined our group. I have collected moths in 19 states and Puerto Rico during the past 12 years. These trips have been made to a wide diversity of habitats, including coastal and inland dunes, pitcher plant bogs, glades, prairies, deserts, western coniferous forests, bottomland forests, upland forests, and many others. In each location and habitat type, I was able to find undescribed species of gelechiids. The memories of being in the field with my "moth-collecting family" will always be treasured.

I became entranced by the microlepidoptera because of their microscopic diversity of the genitalia, mouthparts, and other structures (Figs. 15.7, 15.8, 15.9, and 15.10) and have specialized in Gelechiidae (Fig. 15.11) for the past 15 years.

Fig. 15.6 Whole body of *Machimia tentoriferella* mounted and positioned on two slides

Gelechiidae is originally named from the type genus *Gelechia,* from the Greek meaning "resting on the ground." It is one of the largest families in microlepidoptera and is among the most diverse families in many regions and habitats. Although 4700 species are known and described worldwide (Nieukerken et al. 2011), many species remain to be described. In just the Nearctic Region, there are approximately 870 species present (Lee et al. 2009), but Hodges (1998) estimated that only 30 % of the fauna has been described.

Gelechiids are often referred to as "twirler moths" based on their behavior. Many species will walk around in circles rapidly and repeatedly if they are disturbed while resting on a leaf (or on a sheet). They generally have a wingspan of 7–25 mm, with narrow, fringed wings. Mostly specimens are gray or brown in color and fly at dusk or during the night. A few genera are diurnal. Gelechiids can be differentiated from other microlepidoptera through a combination of following morphological characters, including a hindwing with a sinuous or concave termen and prominent apex and long labial palpus that is curved dorsally, often with ventral brush scales on the second segment (Figs. 15.12 and 15.13).

Larvae have a variety of feeding habits and include leaf miners, gall-inducers or stem borers, feeders within fruits or flowers, and leaf rollers or leaftiers; some are concealed within a larval case or within silken tunnels in the soil (Figs. 15.14, 15.15, 15.16, and 15.17). Some species are known as serious pests—damaging crops or stored food products and causing high economic losses. These include the pink bollworm, Angoumois grain moth, potato tuber moth, and tomato leaf miner.

Fig. 15.7 Confocal laser microscope image of the male genitalia of a new species of genus *Carpatolechia* (Lepidoptera: Gelechiidae)

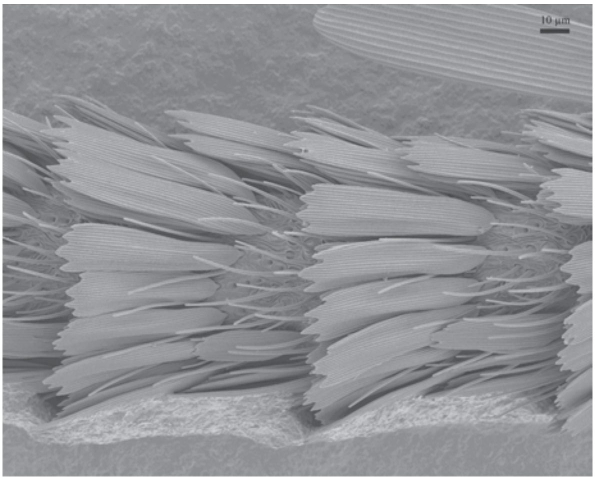


Fig. 15.8 Scanning electronic microscope image of antennal scales of *Sceptea aequepulvella* (Lepidoptera: Autostichidae)

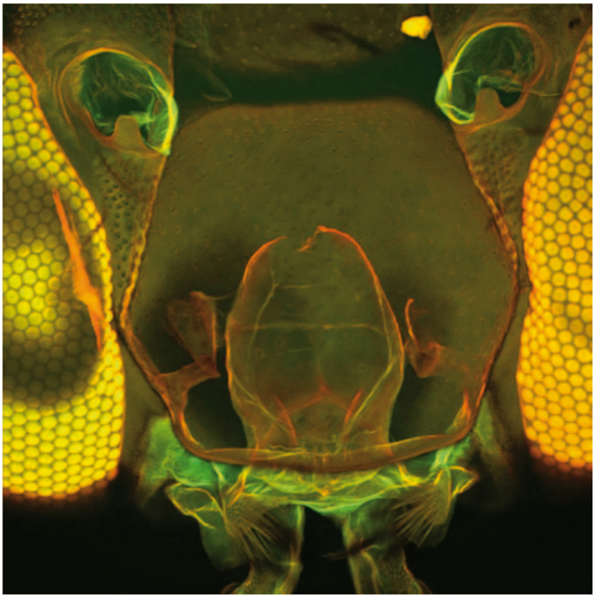


Fig. 15.9 Confocal laser microscope image of the moth head of a new species of genus *Carpatolechia* (Lepidoptera: Gelechiidae)

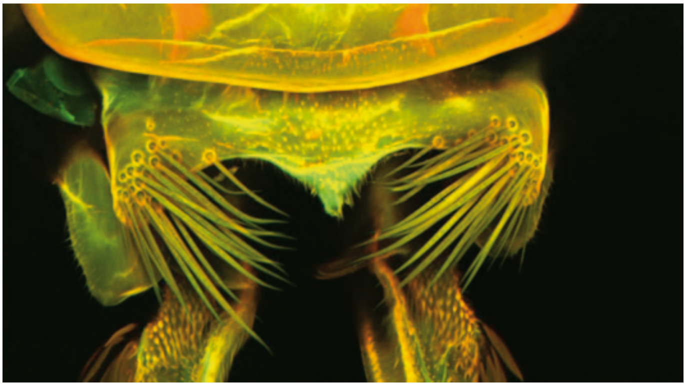


Fig. 15.10 Confocal laser microscope image of the moth mouthpart of a new species of genus *Carpatolechia* (Lepidoptera: Gelechiidae)

I have also worked on some other families in the Gelechioidea. Since 2002 I have curated and identified gelechiids in many collections across North America. I developed a comprehensive Gelechiidae website, which includes images and taxonomical information for general scientists or amateurs and also a Gelechioidea website, which has links to videos on dissecting male and female genitalia as well as collecting and pinning microlepidoptera. During the development of my Gelechiidae website, Bob Patterson asked to use my photos for the Moth Photographers Group (MPG), which he had founded to create a network of people interested in

Fig. 15.11 A drawer of unsorted gelechiid moth specimens

Lepidoptera across North America. He then collaborated with my former advisor, Richard Brown, to move the MPG site to Mississippi State University. Since then, I have been serving as a referee to the MPG site for identifications of gelechiids.

Fig. 15.12 Wings of a gelechiid moth

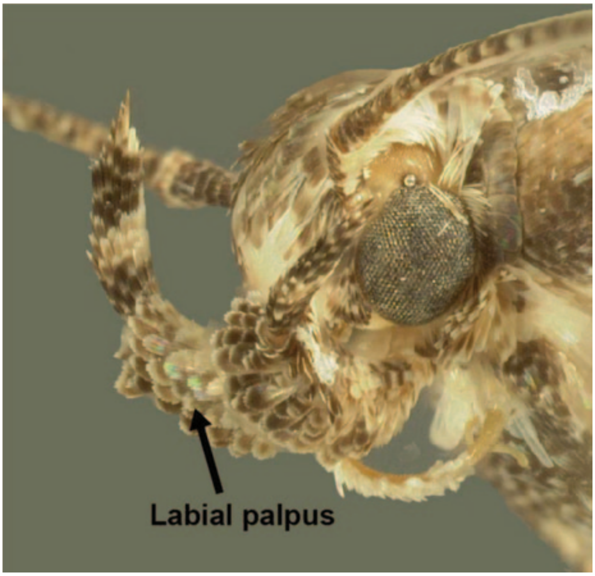


Fig. 15.13 Labial palpus of gelechiid moth

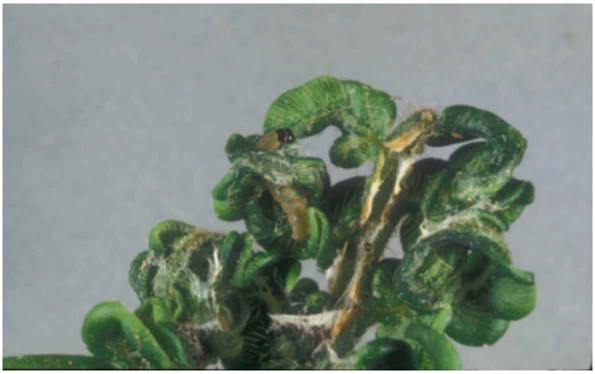


Fig. 15.14 *Monochroa cytisella* larvae feeding in a slight gall in the main stem of a bracken fern. (Photo by Lyle Buss at University of Florida)

Fig. 15.15 *Fascista cercerisella* larvae tying redbud leaves together with silk. (Photo by Lyle Buss at University of Florida)

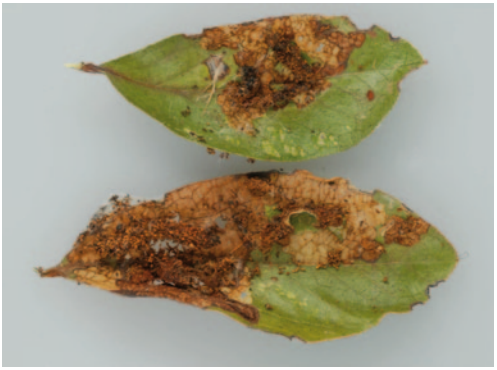


Fig. 15.16 *Aroga trialbamaculella* larvae as leaftiers damaging a blueberry. (Photo by Lyle Buss at University of Florida)

Fig. 15.17 *Sitotroga cerealella* larvae damaging wheat grains. (Photo by Lyle Buss at University of Florida)

I receive many identification requests, mostly by e-mail, with an attached photo of the moth in question, from researchers and amateurs in North America, Europe, and South America and sometimes from India, East Asia, or Africa. One particular example of a correspondent from Mishawaka, Indiana, is worth sharing. I started receiving e-mails from Jim Vargo, an early contributor of photos to the MPG site, before I was involved. His first e-mail asked me to identify a species of *Aristotelia* that was collected near his home. Based on his messages, I could tell that he was a knowledgeable amateur lepidopterist who knew a great deal about moths with a heightened interest in micromoths. In 2008 we finally met, and subsequently, I had the chance to see his amazing collection that included several insect cabinets filled with moths, many of which were well-preserved micromoths. I was astonished by his efforts and by his enthusiasm and knowledge of Lepidoptera that he had learned on his own.

In the beginning of my career with Gelechiidae, my focus was just on working with the species that occur in Korea. Living in the USA for over 13 years of my life has provided the opportunity to work on gelechiids from North and South America. My investigation of the relationships of higher levels of Gelechiidae was a principal study of taxonomy or phylogeny using morphological and molecular data. Now, I am the collection manager of the Hasbrouck Insect Collection at Arizona State

University in Tempe. My interest will continue on the journey of the systematics of gelechiids, with the joy of my pinning micromoths combined with a cup of coffee.

References

Hodges RW (1998) The Gelechioidea. In: Kristensen NP (eds) Handbook of zoology. Lepidoptera, moths and butterflies, vol IV, Part IV. Walter de Gruyter, Berlin, p 491

Lee S, Hodges RW, Brown RL (2009) Checklist of Gelechiidae (Lepidoptera) in America North of Mexico. Zootaxa 2231:1–39

Nieukerken EJ, van Kaila L, Kitching IJ et al (2011) Order Lepidoptera Linnaeus, 1758. (ed. by Z.-Q. Zhang) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148:212–221

Sangmi Lee is a senior research specialist in the School of Life Sciences at Arizona State University (ASU) and has been studying the systematics of Gelechiidae. She also curates the ASU Hasbrouck Insect Collection as the insect collection manager. She was born and raised in a medium-sized city in South Korea and has been living and doing researches in the USA since 2002. She loves collecting or pinning micromoths and also mounting other small insects such as plant hoppers and beetles. She likes to introduce herself as a tiny, little Korean moth girl.

Chapter 16
The Education of the Field Biologist

Michael C. Singer

The work of the butterfly field biologist typically involves travels with humans and larvae interspersed in the same vehicle, spontaneous interrogations from passing strangers or park rangers, and attempts to perform meaningful research in collaboration with disparate personalities at remote sites with no facilities. In the course of this work I believe that I have learned a little about humans, butterflies, and human–butterfly interactions. This chapter aims to transmit some of this knowledge, mostly in the form of mistily recollected anecdotes that I hope will make soothing bedtime reading.

To begin, what ARE butterflies and how did I become involved with them? PUNCH magazine, now long defunct, was not an expected source of scientific advance. Nonetheless, it produced, in the guise of a fictitious village meeting, a highly original classification of butterflies.

Speaker:	"All of Nature is divided into three genera: Animals, Plants and the Weather. The genus Animals is divided into three species: Game, Stock and Vermin. You can only tell them apart after they're dead. If it's bagged, it's Game, if it's insured, it's Stock and if it's exterminated, it's Vermin. Horses and dogs are, of course, Human."
Audience member:	"What about butterflies?"
Speaker:	"Vermin. As far as I know, there are no Game Insects."

Well, that puts butterflies firmly in their place, and to this day it is necessary to classify them as "pests," whether or not they have pestiferous potential, in order to obtain a permit to import them to the USA. But my attraction to them as a child came from the suspicion that like horses and dogs, they WERE human, or almost so. Back in the 1950s, we Yorkshire boys were obliged to wear shorts to school until we were 14, regardless of the weather, so we froze our knees in the Northern winter

M. C. Singer (✉)
Department of Biological and Biomedical Sciences, Plymouth University, Drake Circus, Plymouth PL4 8AA, Devon, UK
e-mail: michael.singer@plymouth.ac.uk

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_16

gales. I regularly arrived at school half-frozen, purple-pimpled, and despondent. My route passed by a few nettle-beds, where, around mid-March, the first butterfly of spring would appear, sitting on the warmest rock and shivering visibly, just like me. So, not only was the butterfly beautiful and a welcome sign of better times to come, it seemed to be feeling the cold just as I was. As a result, by age 9, I expressed a vivid interest in butterflies, to which my grandmother responded: “Butterflies? Very pretty, but what are they FOR?” Nowadays I would answer: “ask a butterfly!” but as a child, I had no answer. In retrospect, Gran would surely have agreed with Punch and casually classified butterflies as Vermin.

I knew that the first Yorkshire butterfly of spring was a small tortoiseshell, because I had a book in which each member of the miserably depauperate UK butterfly fauna was illustrated. However, in the village where I lived, I was unique in this knowledge; butterfly folk taxonomy in rural Yorkshire was little better than Punch’s effort. If a butterfly was white, it was a cabbage butterfly and if it was not, it was a “King George.” If it was small but not white (e.g., a small copper), it was a “Baby King George.” The fact that butterflies don’t grow as adults hadn’t percolated into local knowledge, nor has butterfly biology penetrated much better into the public consciousness in California, where we have repeatedly had this conversation:

“What you doin’?”
“Studying butterflies.”
“Ah. Monarchs.”
“Actually, er, not Monarchs.”
“NOT Monarchs?”

And there the conversation ends, with the inquirer disillusioned at failing to show off their knowledge, and puzzled at our assertion that butterflies exist that are *not* Monarchs. In 2014, I showed a cage of Edith’s checkerspot butterflies to a park ranger in Kings Canyon Park and the ranger said,

“AH, it looks like a Monarch!”
“NO, it isn’t even a bit like a Monarch!
“Yes it is, it’s orange!”
“It’s the wrong size.”
“Couldn’t it be a baby Monarch?”

Traveling with Larvae

As I write in 2014, I am preparing a vacation with my spouse, Camille Parmesan, a climate-change biologist, and I have been made to promise that there will be NO BUTTERFLIES. Why might this be important? Camille has a long memory. Back in 1999, we traveled too extensively with 1000 Finnish Glanville Fritillary larvae. We began by raising the larvae in Texas until they entered their winter resting stage in summer 1998. In spring 1999, we took them to Montpellier (the one in France), woke them up, and fed them in a campsite (see *“biologists are nerds”* account in a later section). Then we set out to drive them to Finland for an experiment. As the larvae grew, the task of feeding them became more intensive and they occupied more space in our caravan. In the USA, this vehicle would be called a travel-trailer; I do understand that to Americans a "caravan" is either a motor vehicle or a line of camels. But I am describing events in Europe, so the caterpillars are traveling in a caravan.

The caravan had two beds, one for us and one for the larvae. But larvae would occasionally escape and turn up in our bed. Oddly, although the larvae were more furry than slimy, this still seemed to bother Camille. Somewhere in Northern France, it happened once too often. "You're not going to do this AGAIN, are you?" she said, and although it was phrased as a question, it was not. But soon afterwards she flew from Amsterdam to California leaving me, the caravan, and the larvae to complete the trip to Finland. Unfortunately, there was a heatwave in Sweden and although I had timed my larvae to become adults just as I arrived in Finland, the heat speeded them up, and I quickly had at least a couple of hundred butterflies. Butterflies need more care than larvae or pupae, so I had to spend much of the day feeding them and then travel at night, pretty tiring! And then the ferry from Stockholm to Finland was booked for a week and I couldn't get on it. For a few days, I camped out in the car park (parking lot to the US readers) of the Zoology Dept of Stockholm University, visible from the faculty office windows and apparently causing considerable entertainment. With the butterflies quickly aging in the heat (no air conditioner in the caravan!), I went back to the ferry office waving several cages full of them. I said "These little Finnish butterflies have come all the way from Texas, they need to go HOME and they will all DIE here on this dockside if you don't let me on the boat!"

They did let me on the boat and I soon arrived at the Finnish field station, Tvarminne, where both I and the butterflies were greeted with memorable sangfroid by my friend and fellow checkerspot biologist Ilkka Hanski. In order to explain the remarkable nature of this greeting, I need to describe the experiments that had been planned, both mine and Ilkka's. We already knew that Glanville Fritillaries inherited different oviposition preferences, that is, different preferences for plants on which to lay their eggs. My plan was to release butterflies with different preferences in artificial habitat patches and see how the plant composition of the patch influenced the tendency of the insects to emigrate. The Finns were planning a quite different experiment; they had raised Glanville Fritillaries that they were planning to use to create inbred matings (brother–sister) and outbred matings (between insects from different populations). They would then start new populations in the field with inbred and outbred insects to see the effect of inbreeding on the growth and survival of those populations.

In the early part of the trip, when Camille and I had reached Central France with our caravan load of caterpillars, I had called Ilkka, told him that I planned to arrive with 1000 butterflies and asked him to make up the artificial habitat patches. Now, I claim no ability to decipher Finnish emotion, especially over the phone, but it was clear that there was some kind of emotional response to my call, although I couldn't tell what KIND of emotion was involved. Later it materialized that the emotion was amusement; there was considerable dinner-table laughter at the field station in Tvarminne at the thought of Singer struggling from the Mediterranean to the Baltic with a decrepit car[1] hauling an even more decrepit caravan[2] full of 1000 Glanville Fritillaries.

The Latin name of the Glanville Fritillary is *Melitaea cinxia*. Latin names are supposed to foster international comprehensibility, but "cinxia" is pronounced "sahnxIA" by the French, "thEEnkthia" in Thpain, "SInksia" in England, and "kEEnksia" in Finland. Not much comprehensibility there, but since the larvae were from Finland I referred to them as "keenskia." Therefore, when I got to Sweden and was overwhelmed by emerging butterfies, I called Ilkka again and said: "Ilkka, I have TOO MANY butterflies, I'm feeling increasing KEENKSIA PRESSURE here, I'm going to need HELP when I get to Tvarminne!" I felt another Finnish emotional response, but I couldn't tell whether it was the same emotion. It was not. In the time between my two calls, a disease had struck the keenksia cultures and a small army of postdocs assembled to experiment on the expected butterflies was sadly contemplating tray after tray of dead pupae. So, the conversation at dinner evidently changed from "HAHA! Did Singer REALLY say he's going to arrive with 1000 butterflies?!!" to "Hmm… if Singer DOES arrive with 1000 butterflies, what's the chance that he can be diverted from that boring experiment he's planning into something more interesting, perhaps, for example, an inbreeding experiment?"

When I arrived at Tvarminne, Ilkka opened the door of the caravan and silently contemplated the dirty makeshift rearing containers, mostly decapitated Evian bottles, in which emerging butterflies were crawling up out of the messes of dried food and larval frass. Hanging from the roof were dirty net cages in which hundreds of adult *cinxia* were bouncing around. Ilkka thought for a while and said: "Keenksia pressure should be measured in Mikes. One thousand keenksia in a caravan makes one Mike of keenksia pressure. Unfortunately we are suffering only microMikes of keenksia pressure here at Tvarminne…………(hesitation)…….This experiment you are planning……………… would it be completely incompatible with a SMALL…….er…….INBREEDING experiment?"

Hence, we did what seemed to me to be a LARGE inbreeding experiment, though to Ilkka it may have seemed small, he thinks on a bigger scale than I. In recognition of this difference in the scale of our thinking, I long ago christened him the "King of the Keenksias," an alliteration that I find appealing. To consolidate this classification, I presented him with a mug bearing the inscription "Ilkka I, Dei Gratia

[1] The car had been purchased from a very fast-talking prison guard whose friend explained to us, *sotto voce*, that he had bought the BMW to impress women and that it had worked TOO WELL, so he had to sell it for quick cash and buy a 2CV. We had the impression that he was married and his girlfriend was pregnant.

[2] The caravan had been purchased from a man in the throes of a nasty divorce; he had hidden it in a refrigerated fish warehouse to prevent his wife from selling it; we suffered a series of jokes about how well preserved it must be until Camille's collaborator in Sweden, Nils Ryrholm, suggested that we park it in the multistory where he kept his car. He cheerfully waved us in, but the caravan was too high and the ventilator on top was chopped off, subsequently admitting rain to the wooden inner structure. After a winter in the UK, I attempted to drive the caravan to southern France, but inspection in the mirror soon revealed that, the faster I drove, the WIDER the caravan became. SIGH.

Rex Cinxiarum" and notepaper headed "In Cinxia Veritas," my imagined traditional motto for the Kings of the keenksias.

Ilkka was pleased with the results of the inbreeding experiments and even offered to make me vice-king of the keenksias if I could answer a "simple keenksia puzzle." Alas, I could not answer it, and to this day I can claim no official title with respect to keenksias, or, indeed, any other butterfly.

In the course of doing the "small" inbreeding experiment, I explained to Ilkka that Camille had quite forcefully declined to repeat the experience of traveling with 1000 larvae. Ilkka said: "Ah, Mike! If you like, I will find you a wife who will not complain about the caterpillars in the caravan." What a sweet offer! And, given the history of my interactions with Ilkka, I was sure that he was quite serious and prepared to put himself out to find me such a wife. Why was I so sure? The first time I had met Ilkka, he had asked what I was planning for the next year.

> "I'm hoping to take a visiting professorship in France."
> "Where in France?"
> "Tours."
> "Why don't you go to Montpellier, it's a better department?"
> "Ilkka, there's a SIMPLE reason why I'm going to Tours and not Montpellier. The people in Tours have invited me and the people in Montpellier have not."
> "One moment, I will arrange it."

And arrange it he did, returning after what seemed like 20 min with a faxed invitation from Isabelle Olivieri for me to be a visiting professor in Montpellier, a university with which Camille and I have been happily associated ever since. So, when Ilkka offers to find me a wife who won't complain about the caterpillars in the caravan, I have to take this offer seriously. As it turns out, I've been very happily married and have had no need to take up this fine offer, but I became puzzled at the ease with which Ilkka seemed to think it could be done. A few years ago, I sent a brief message: "Ilkka, although I haven't yet asked you to take any action, I haven't forgotten your very kind offer about the wife. However, since you made that offer I've met quite a few Finnish women and they all seem pretty forceful, so I begin to wonder how you proposed to find one who would not complain about the caterpillars." I received a terse Finnish reply: "We said nothing about the nationality of the wife."

Encounters with Unexpectedly Knowledgeable People

While traveling in France, I came across a small group of apparent amateur naturalists examining a butterfly and seeming to try to identify it. I said "I'm a butterfly biologist, and isn't that *Brintesia circe*?" A Frenchman replied, with undisguised scorn and disbelief, "You're a BUTTERFLY BIOLOGIST??! No, it isn't *Brintesia circe*, it's *Hipparchia fagi*, and you can't identify it without examining the genitalia."

How embarrassing! Fortunately, I knew from past observation that this can happen to the best among us. Back in 1970 or 1971, Larry Gilbert and I accompanied

Paul Ehrlich, our PhD supervisor, to the Del Puerto canyon population of Edith's checkerspot, situated in the most desolate part of that canyon, not far from where we were informed that a 1950s rock musician had been killed and lain undetected for nearly 20 years. Despite the remoteness of the site, a little old woman materialized and said, "Are you Paul Ehrlich?" When Paul confessed his identity, happy to be so well known, her tone became quite aggressive. "I've got a BONE to pick with you!" she said. "In the very front of your book you have a drawing of a *Danaus plexippus* larva with appendages labeled OSMATERIA! What a silly mistake! It's not a swallowtail, now, is it? " Having said her piece and apparently having no further desire for exchange of information with Paul, she wandered off. On my return to Stanford, I checked in Paul and Anne's book. Indeed, the little old woman was correct.

A few years later, in 1981, I was struggling to publish enough to gain tenure at the University of Texas. My friend and colleague Larry Gilbert advised me to stop doing research and just write. Against his advice, I took off to California with my students, stopping off at Stanford to give a talk. At Stanford, Paul gave me exactly the same advice… go back to Texas and WRITE! I remonstrated that I didn't want to write up results prematurely, I wanted to wait until I was reasonably sure that they were correct. Paul said: "With that attitude you're sure to be FIRED! You're throwing the baby out with the bathwater!"

Well, I didn't like this advice and I am stubborn, so I drove up to Sequoia National Park with my students, Rick and Sandy. After a few days of fieldwork we needed showers, so went to the nearest shower at Stony Creek. There was only one shower working, so Rick and I waited in the truck while Sandy took her shower. A dirty white Toyota pickup pulled up next to us, with a little old guy in a floppy hat. He squinted at the decal on our truck door and said, sounding a bit drunk:

"Univershity o' Texash, eh?"
"Yes"
"Cher doin?"
"Studying butterflies"
"You a shtoodent?"
"No, I'm a professor."
"OH, ye're REALLY shtudyin 'em, eh?"
"Yes"
"You learn somethin' new every day……………DO YER?"
"I tell myself that I do."
"Yeah, but does it appear in PRINT?"
"Er…sometimes it does and sometimes it doesn't."
"If it don't appear in print, it ain't worth a damn!"

And with that he drove off, leaving Rick paralyzed with laughter in the back of our truck. WHAT?! HELP!! WHO SENT that man?

After another few years, I drove into that same Sequoia National Park with my undergrad research assistant, Marie Butcher. As we were descending from our truck, a park ranger appeared:

Ranger: "BUTTERFLY…. nets??!!…… In a NATIONAL….PARK???"
Singer: "Would you like to see our…….PERMITS?"

Ranger: "yes…." (examines permit) "so what exactly are you doing?"

Singer: "Marie is going to climb to Colony Meadow and start catching female Edith's checkerspot butterflies at 3 p.m. I'm going to drive to Rabbit Meadow and also start catching at 3 p.m. That way, the butterflies from the two origins will have been held captive for the same length of time when we start to test their preferences tomorrow afternoon."

Ranger: "Let me get this straight. SHE'S going to hike up 1500 feet in elevation through thick brush with no trails, and YOU are going to just DRIVE to where you can catch the butterflies? And I expect you're going to be the senior author of the paper and she'll be the junior author, am I right?"

Singer: "er……yeah."

And, much later, I was.

Southern California Lives up to Its Reputation

March, 2009. Here we are, Camille and Mike, in Southern California on a field trip to catch a few individuals of the Quino checkerspot butterfly for genetic analysis. A VERY few, because it's a Federally Endangered Species. Time to put on some field clothes and catch butterflies. But do I really need to exchange my comfy sandals for those nasty tight boots just because of the possibility of encountering snakes? Just because LAST time I went hiking in these hills, Camille watched me from a distance and saw me hop high in the air on one foot. She wondered how a person could hop that high and why anyone would suddenly do that. The reason was that the other foot was descending onto a writhing rattlesnake and the only way to avoid direct contact was to hop away on the foot that was not headed for the snake.

So should I worry about snakes today, enough to change shoes? Naw, I can watch out for those snakes, the hilltop is almost bare, nowhere for them to hide. And that is true, but I don't seem to be very good at watching for snakes and butterflies at the same time, so AAAAKHH! I end up in my sandals less than 2 ft from a big rattler poised to strike and rattling away at me. I don't have time to be scared, I just back away and the rattler calms right down. How nice, a mellow rattlesnake! But OK, I'd better change shoes.

Next day, a drive across Otay Mountain with Joyce, Mike (the 2nd), and Chris, all come out to help and advise. Mike-2 knows where he has found the butterflies, which turns out to be the exact spot where Camille had found them in 1996. Great! Right up against the Mexican border, we can see the fence! A few old male checkerspots are patrolling the hilltops and it looks to be late enough in the season that the females will all have found mates so, from the conservation point of view (if not from their own), those old males are useless and can be caught so that their genes can be removed.

We have a problem. For perhaps the same reason why I am not very efficient at maintaining vigilance against snakes while searching for butterflies, butterflies aren't very good at maintaining vigilance against people while chasing mates or drinking nectar. So the best way to catch them is to find them concentrating on feeding. Even better, find a male concentrating his few neurons on courtship and a female concentrating on rebuffing him and you can often very easily catch them both with one sweep of your net. BUT the butterflies here today seem all to be males and the nectar supply is good, so those males have tanked up and fed as much as they need. They are sitting on the ground in exposed positions watching for anything to approach. And it is VERY hard to approach them close enough to catch them. The closer you get, the better they can detect your movement, so slower you have to move. Until your final strike, that is. Moving even more slowly as you approach, doesn't FEEL like the right way to do it, but it is.

Chris sees a butterfly and follows it till it arrives near Mike-2, who follows it till it arrives near Camille, who follows it till it arrives near Joyce, whereupon it alights on a rock on the very top of the hill and poses there for a vigilant rest. For some unknown reason, I have the only butterfly net, so there is a chorus of folk hollering at me to come back up the hill FAST! I do my best and arrive panting. Joyce is standing frozen, but she can move her mouth to tell me where the butterfly is. Once I have seen it, I circle around and approach it with the sun almost in front of me and my shadow behind me, so that the butterfly won't see the shadow. Four people are standing absolutely still, each in a different body position, while the fifth person, me, attempts to glide imperceptibly (from the butterfly perspective) towards my prey. It takes several minutes for me to inch to a position where I can start to ask myself if I am close enough to strike (like a rattlesnake?). And I am NEARLY close enough but NOT QUITE when a HUMAN HEAD appears over the brow of the hill. I can see it by rotating my eyes without moving my head, cos if I move my head the butterfly might detect me. I see with my rotated eyes that it is THE BORDER PATROL!

No surprise, we are right next to the border. Joyce and Mike say that someone had better DO something before the Border Patrol scares the butterfly. Camille says, in her most authoritative tone: "Please STOP RIGHT THERE sir!!!" with all the emphasis on the "stop" rather than the "please" or the "sir." Amazingly, he does! Perhaps he stops more out of astonishment than anything, because I don't imagine that people normally address the Border Patrol in that tone or anything remotely like it. But it works. Instead of going for his gun the Border Patrol asks quite mildly what we are doing and Mike-2 starts to explain: "We've got an endangered butterfly here, we can't move until this gentleman catches it." After a pregnant pause, the Border Guard asks how long we'll be here. "Just as soon as we get this butterfly," replies Mike-2. The guard keeps his composure, and ends with "We've got a bunch of people coming this way in a few minutes—you might need to watch out," and, thankfully, departs. At that very moment, I feel that I am close enough to strike and indeed I am!!! THREE males in the bag.

The Border Patrol is gone, and it's time for a beer. What to do in San Diego of an evening? Where is the center of attraction for the locals? It is the WAVE HOUSE. Neither of us has seen or heard of a wave house, which shows how out of touch we are with reality, California style. For the Wave House contains a real wave! Just one, but really a quite splendid one, a life-sized ocean breaker, maybe 10-ft tall and curled over into a "pipeline" for about half its length, crashing down over itself and breaking up into a chaos of bouncing, foaming surf. The other half is a big hump of a wave that simulates one just about to break.

A man in a wetsuit is surfing the wave by switching back and forth over the hump just as you'd do in the ocean. Then he changes tactic, hovering halfway up the wave in the mouth of the pipeline. URK! He's sucked into the interior of the pipe and totally disappears. Is this dangerous? Whether or not it is, it looks so, which is sociologically necessary (see below)! But in fact he's OK, after about a minute he wipes out and is spat into the foaming surf at the base of the breaker in a whirl of flailing limbs.

Part of the wavehouse is a pub, from which you can sip your beer and watch the action. The other part is the enclosure containing the wave. It's fenced off, but you can see through the fence just fine. Just on the other side of the fence, with a ringside view of the wave and the surfers, is a hot tub. This is essential to the sociological aspect of the wave house, which evidently mimics California culture in more than just the surfing. To enter the enclosure you need to be admitted by the Guardians of the Wave. They seem also to be, in practice if not in name, Guardians of Traditional California Beach Culture. To pass their inspection you need to be either a Surfer (male) or a California Cutie (female). If you are a Surfer, once admitted you line up to ride the wave. If you are a Cutie you stroll over to the hot tub, shimmer out of your shawl, strut around in your bikini for a few moments, then hop in the tub and admire the surfers seeming to risk their lives. The Guardians don't allow more than one surfer on the wave at the same time but they do let several Cuties into the hot tub. Can Cuties try riding the wave? In theory I expect so, but we didn't see it. Can surfers get into the hot tub to relax? Very rarely, but they seemed less intent on warming up than on having a quick flirt before heading back into the line. Back to the sixties, eh?

Hitchhikers

Friday, May 14, 2004. I'm driving from Austin to Fresno for fieldwork in the Sierra Nevada. Somewhere West of Phoenix Marcel, a very tanned fellow asks if I have a gas can he could borrow cos he's out of gas a mile back along the freeway to the West.

Marcel: Man, I'm so looking forward to this, I'm going to Phoenix to propose to a wonderful woman. Shelley. If she's still alive, that is. It's just so slow trying to get there, running out of gas every few miles and having to bum a couple bucks to get a few miles further. Shelley's just wonderful, she'll put me right. If she's still alive. I got lots of friends in Phoenix, I'll be OK if I can just get there.

Mike: It's not that far to Phoenix, why don't you give Shelley a call and have her come out to pick you up?

Marcel: Don't have her number

Mike: You are going to propose to her, you expect her to say 'yes' but she didn't give you her phone number? I'm not sure that your prospects are wonderful.

Marcel: Oh, she DID give me her number but I threw it away a year ago, I was dealing crack cocaine then, my life's path was different. But we agreed that if we ever met again we'd go to DC and get married. I just hope she's still alive.

Hmmm, well, that was the oddest interaction I've had with a hitchhiker in the USA since that LAST time I picked up a hitchhiker in the USA, which was back in 1995. Why has it been so long? After what happened to me in 1995 I had promised Camille to pick up no more hitchhikers. Ironic, really, because that summer I had been worried about Camille, working out in the desert for months at a time and sleeping in her pickup truck. But nothing had happened to her at all, and this is what had happened to ME. I gave a ride to a young hitchhiker out in the desert on Hwy 395 south of Bishop. I did it because she had blood streaming down her face and was carrying nothing but a small dog; seemed as though she might be in real trouble. And, indeed, she told me she had been attacked and wanted to be taken to hospital.

When we got to Bishop I asked at a gas station how to find the hospital. While we were driving there the woman held up her dog vertically, facing her, and put out her tongue at it. The dog, evidently familiar with the procedure, put out its own tongue and touched the tip of hers with it. Then they both vibrated their tongues up and down with astonishing speed, they made a tongue blur between them. I can still picture it in my mind, it was extraordinary. As I dropped the woman off at the hospital, a nurse came out. The woman took one look at the nurse and ran away. The nurse ran up to me and said, in a very worried tone:

> "Are you all right?"
> "I'm fine, but SHE says she's been attacked and she needs help, her face is bleeding."
> "HA! Help indeed! Only reason her face is bleeding is she's so high on speed she's scratched her own face off! You are VERY lucky, that's a very violent person, last time she was in here she injured six nurses!"

OK, from here on out my attitude to hitchhikers is country-specific. No more US hitchhikers! In the past 10 years, I have picked up three or four hitchhikers in France, all of whom turned out to be law students or grad students commuting between home and college. They were all normal, interesting, informative people and I learned a few things from them.

On the other hand, here's what happened when I picked up a hitchhiker in Trinidad in the early 1980s. I should say that in Trinidad only about one driver in 200 was white, at least back then, I dunno how it is now. So I was an odd color. I stopped to pick up a guy who was wearing a very decorative outfit. He looked at me very hard and hesitated about getting into the car. He didn't say much but as I was preparing to drop him off he said:

> Man, I gotta hand it to you, you sure got guts!

I didn't understand at all, but it later became clear that had I been possessed of any local knowledge at all, I would have realized from his dress that he was a member of a movement dedicated to removing every single white person from the island, by killing them if necessary.

I didn't have guts, I was just ignorant, but I made a VERY good impression!

I have only picked up one hitchhiker in England and that was odd, but not dangerous, at least not to me. I picked up a woman, probably partly because she was exceptionally beautiful and I worried that it might not be safe for her to be hitchhiking. Well, also I thought she might have some emergency, she was very smartly dressed, not dressed for hitchhiking. It turned out that she had no emergency at all and the strong impression I got was that she was hitchhiking because SHE thought it was dangerous and a little danger was exactly what she had in mind. I also got the strong impression that I was a complete disappointment to her.

Ah, well…. Onwards to Fresno, let's see if I can disappoint someone there!

Butterfly Biologists Are Nerds, Butterfly Biologists Know Nothing About Real-Life and Personal Relationships

Brigitte and Patrick ran the Camping Pic St Loup, north of Montpellier. Brigitte gradually became more and more annoyed with me because I was busily feeding 1000 Finnish caterpillars (see above!) and paying no attention to Patrick's flirting with Camille. So Brigitte approached me at my work.

Brigitte:	What are you doing? (qu'est-ce que vous faites?')
Mike:	Feeding my caterpillars ("je soigne mes chenilles")
Brigitte:	WHY?? ("pourquoi?")
Mike:	Because I know that in France there is a saying that a man, to be a REAL man, must take *excellent* care of his caterpillars. ("parce-que je sais qu'en France on dit qu'un homme, pour etre un VRAI homme, doit *bien* soigner ses chenilles!")
Brigitte (with disgust):	A man who takes excellent care of his **caterpillars** does not have time for his WOMAN! ("un homme qui soigne bien ses **chenilles** n'a pas assez de temps pour sa **femme!**")

Years later, I recounted this event to our Mexican field assistant, Alina Cepeda, in Kings Canyon Park, where I was part of a small group working on a complex and difficult project devised by my friend and colleague Lindy McBride, from UC Davis. Soon after I had told this French story to Alina, she and I were trying to leave camp for a food-shopping trip to Fresno but I wanted to feed some old butterflies before leaving and I couldn't find them. Eventually I gave up, we had to leave without feeding those butterflies or we wouldn't be back by midnight. Alina had an incisive comment:

> So, Mike, jew are not caring for jour butterflies and jour wife is in Texas, it is NOT like jew told the woman in France, is it? Jew are not caring for jour butterflies or for jour woman!

I was sufficiently disconcerted by this comment that I started up the truck with the brake on. Alina spotted this immediately:

Mike, the brake is on, jew are not caring for jour TRUCK, jour WOMAN or jour BUTTERFLIES, Mike this is jour ENTIRE LIFE that jew are neglecting!

O dear…

Alina was outgoing, cheerful, and funny. She was a Buddhist and looked perhaps more Russian than Mexican, auburn haired, and green eyed. Beautiful, in fact. Well, of course, that's a matter of opinion but let's just note that when Alina and I went food shopping in Fresno, the guys in the store perceived immediately that I was too old to carry the food to the truck. When I did the shopping alone, I somehow seemed to be younger. So, perhaps it was no bad thing that Alina quickly developed the opinion of me as a total nerd. I would worry about the health of my caterpillars; I would slow down the truck to point out a nice patch of *Collinsia* plants (caterpillar food). Alina quite tartly suggested that I was not a real man, I knew nothing about real life, only about *Collinsia* plants. I admit that I played up to my nerd image a bit. When the fellow on "Radio Amor" sang "quarenta y veinte," a song ostensibly by a 40-year-old man trying to impress a 20-year-old woman, one of his pick-up lines ran "tengo muchas vivencias." I said to Alina that I wasn't familiar with the word "vivencias," but that I assumed it meant little living things and that he might be singing about the caterpillars that he was raising. Alina, in disgust, corrected me: "it's LIFE EXPERIENCES, Mike." My image as a nerd was confirmed.

Alina had little experience of the USA so I told her some tales of the culture, among them the fact that many of my nonscience students in Texas worried about me, I seemed like a nice person but I was surely going to HELL for teaching them evolution.

A couple of days later, I drove Alina to get a shower at the Park Headquarters (our camp had no water supply) and on the way back we stopped to admire the almost-full moon flooding the silent forest landscape. We stood on the side of the road with the moon behind us, its light spilling past us down the mountainside towards the glimmering lights of Fresno 7000 ft below us. A romantic atmosphere! So, I admit that I had a small "Jimmy Carter moment." (Long ago, when he was President, Carter was asked in a Playboy interview if he had been unfaithful to his wife and he replied that he had occasionally lusted in his HEART). Anyhow, if I might have had a momentary thought that a moonlight kiss would be nice, it was immediately followed by the twin realizations that

1) I was 62, Alina was 26, so any such suggestion would almost certainly disgust her, and
2) that if by chance Alina were not disgusted, then Camille would certainly be!

But the moonlight required SOME comment, so what I said was deliberately UNromantic, holding to my nerdy image.

Mike: "what wonderful moonlight, you could, er, ….gather *Collinsias* by it."

Alina: "Mike, that is NOT a good use of moonlight! And jour students are wrong about jew, jew are not going to HELL, jew are going to HEAVEN where jew will gather *Collinsias* by moonlight for ALL ETERNITY!"

Er, I surely hope not! And I have never before or since been condemned to heaven in a tone that implied it was a punishment. But punishment is clearly what Alina had in mind.

The Intellectual Acumen of Butterflies as Study Organisms

In the course of this account, I have occasionally been less than complimentary about the character and intellect of individual humans I've encountered in my travels. So it's only fair that I should do the same for the butterflies I've studied, especially my study checkerspots, genus *Euphydryas,* cheerfully abbreviated by Chris Thomas as "Euphies." However, my first introduction to butterfly intelligence was with the tropical genus *Heliconius*. My supervisor, Paul Ehrlich, had, on advice from Philip Sheppard, decided to do a population dynamic study of *Heliconius* in collaboration with my friend and fellow student, Larry Gilbert. As a result, Larry kept a greenhouse full of these butterflies on the roof of the Stanford biology labs. On the first day of its life, a *Heliconius* would occasionally bump into the glass, but it soon learned not to do that, after which it could be watched, much like a tropical fish in an aquarium, navigating around in a seemingly natural, if confined, manner and performing its normal behavior patterns—seeking mates or nectar, or places to bask—to oviposit or to roost communally for the night.

I should have had some warning that "Euphies" have limited mental capacity, even for butterflies. Watching them in the field, I had observed that when they achieved very high density, the males spiralled around each other so frequently that they wore their wings shorter and shorter until they could hardly fly at all and as each female glided past she was followed by a wave of males jumping off the flowers, flapping their wing stubs vigorously, going nowhere and falling back almost exactly whence they had started. I ignored this warning and tried to study Euphy flight behavior by releasing my butterflies in the Stanford greenhouses alongside the *Heliconius,* where the Euphies simply beat their brains out on the walls until there remained neither brain with which they might learn not to do that or sense organs that might detect the glass. So it wasn't possible to study natural flight behavior of these butterflies (or their relatives) in captivity, you would either need to do it with the insects completely at liberty or build an ENORMOUS cage—which has been done—but by Finns and Swedes, not by me. As a result of my failure to study Euphy flight in captive butterflies, I developed a bad case of *Heliconius* envy, from which I have never completely recovered.

One of the intellectual differences between *Heliconius* and Euphies is actually useful to the Euphy biologist. If you gently place a male *Heliconius* behind a female, he will not court her, he will fly off; if you place a female *Heliconius* on a

Fig. 16.1 With a mating pair of Marsh Fritillary butterflies on each finger, the author demonstrates their docility and manipulability

host plant, she will not assess it for oviposition (egg-laying) as if she had alighted on it naturally, she will just fly away. She won't accept a human to interfere so rudely in her normal behavioral sequences. In contrast, Euphies can be quite calm when handled and undeterred from their normal activities (Fig. 16.1). A Euphy male placed behind a female may court her and a female placed on a host will consider whether or not to lay eggs on it, just as though they had alighted naturally at the sites where they were placed. By staging encounters like this you can ask a female for her opinion about a plant as a potential site for her eggs, just by placing her on the plant and observing her response. And if you prevent her from actually laying eggs each time she has decided to do so, you can ask her opinion over and over and over and over again and measure how the range of plants she would accept increases as time passes, much as the range of foods acceptable to a human would increase if the human were repeatedly shown a series of food items but not allowed to feed. When performed with Euphies rather than humans, this experiment gives consistent results, the insects don't seem to get bored with the procedure and don't indulge in any kind of learning that might complicate the experiment. Indeed their oviposition preferences are strongly inherited, through both male and female lines. Even though the males don't lay eggs, they have genes that affect their daughter's preferences.

Does this manipulability of Euphies make them easier to raise and culture? In theory, perhaps. If you place an adult Euphy on a sponge soaked with dilute honey, the butterfly will taste the honey with its feet and uncurl its proboscis to feed. This SHOULD make them easy to feed, and it IS easy to feed a small number of them. However, when I was tasked by Lindy with feeding a large number of males in order to keep them in good health and available for mating, I discovered a new set of limitations arising from the butterflies' limited mental capacity. We had fewer cages than males, so we had to keep at least half a dozen males in each cage. Even though the cages were small (25 cm × 25 cm), the butterflies seemed unable to find food placed in their cage, so each male had to be gently and individually lowered onto the sponge feeding pad until he tasted the honey with his feet and began to unfurl his proboscis. This could work out OK unless the butterfly saw a bird flying by, in which case he would take off to chase the bird and crash into the side of the cage.

Fig. 16.2 Freestyle oviposition

If the male did feed, I would add another male to the opposite side of the pad so as to feed more than one at a time, but this risked the second male running over and trying to copulate with the first male, driving him off the food. The most frustrating and least expected obstacle was that a male would attempt to copulate with the feeding pad itself, driving his genitalia into the sponge and pushing himself up on tiptoe so that when he unrolled his proboscis, it waved around in the air uselessly and couldn't reach the sponge. This happened so often that I felt obliged to release my frustration in doggerel:

The Euphy male's captivity won't dampen his lascivity
but the release of his passions distracts him from his rations
and he dies in a dither
in a hyperactive daze
never pausing to consider
the error of his ways

Not that the females are clearly smarter than the males, see Fig. 16.2. Alas, this is not an example of sophisticated maternal care; she is not protecting her kiddies from their enemies because she will not survive until the eggs hatch. I sent this pic to Ilkka, titled "IDIOT BUTTERFLY," but Ilkka replied that I clearly did not understand my own study organism—she was practising her Freestyle Oviposition—a recognized side-event at the Olympics. I'm not totally convinced that Ilkka is correct about this, but his comment does remind me to be less anthropo-superior in my global view. If current trends continue, our intelligently organized civilizations may crumble, but whether or not they do, I'd bet that the Euphies will still be around.

Michael C. Singer was educated at Oxford and Stanford and is currently a Professor of Evolutionary Ecology at Plymouth University. At Oxford he was initiated into butterfly evolution by E. B. Ford and into butterfly behaviour by Niko Tinbergen. Singer remembers Tinbergen describing an experiment in which he presented cabbage butterflies with different-colored discs to study their attraction to flowers when nectaring. However, the butterflies paid no attention at all to the discs until one day, they swooped down on them just after Tinbergen had entered the enclosure. Tinbergen eventually realized that this was because he had just kissed his wife, who was wearing perfume. This appealing anecdote helped Singer develop an interest in butterfly behavior, which led him to a PhD at Stanford under Paul Ehrlich, a contributor to this volume. At Stanford Singer collaborated with Larry Gilbert (see HIS chapter). Singer has been inducted into metapopulation ecology by his collaborations with Chris Thomas and Ilkka Hanski (see HIS chapter), into speciation biology by collaboration with Carolyn Mcbride, and into global change biology by collaboration with his spouse of over 30 years, Camille Parmesan. Michael C. Singer is not the same person as Mike Singer The Younger, Michael S Singer, who performs excellent research on evolutionary ecology of Lepidopteran diet.

Part VI
History

They're dainty little creatures that hardly exist at all: they come out of nowhere, search quietly for a few, limited things, and disappear into nothingness again, perhaps to some other world.
H Murakami, *1Q84*

The life of a butterfly is short. By comparison, the life of a lepidopterist is long, and full of history. The chapters in this last section could have appeared in other parts of the book, but have a certain scope of experience and time that makes them a fitting place to end. A historical perspective reminds us that the scientifically-minded pursuit of butterflies and moths is really not more than a few generations old, which is to say that there is much more to be learned.

MLF

Illustration by Su'ad Yoon

Chapter 17
Some Brazilian Lepidopterists

Ivone Rezende Diniz

My initial indecision on whether or not I was qualified to contribute to this book was partly because of my view of myself as a scientist: Am I a lepidopterist, or more a general ecologist or entomologist? Because of this reasonable doubt, I decided to present a lepidopteran view from some lepidopterists who worked in the past or have worked for a long time in Brazil, and then to end with, a personal account of the research adventures experienced by myself and my colleague, *Helena Castanheira de Morais*. These latter adventures were centered in Brasilia and were associated with our pioneering work on large-scale caterpillar surveys and ecological studies in the Cerrado (Brazilian savanna). This chapter is certainly not intended to be a review of Lepidoptera research in Brazil, nor is it a history of its researchers. Rather, I decided to mention some of the lepidopterists who are considered to be important for the advancement of Lepidoptera knowledge in Brazil. Thus, for brevity, among other reasons, I have omitted many important names of Brazilian lepidopterists—for example, the applied lepidopterists, who are dedicated and devoted to studying pest species in agriculture.

I will start by saying that finding diversity for any taxon is not a problem for academic Lepidopterists in Brazil; in fact, it is an inevitable and welcome complication of our research. Over the years of collecting caterpillars, Helena and I have always agreed that the biodiversity of these creatures is amazing and every caterpillar-collecting or research venture produces another unknown or beautiful cohort of specimens, but the curiosity and interest that come from these discoveries also prevent us from carefully developing all the studies and experiments of our dreams.

What are our estimates of diversity? Of the estimated number of Lepidoptera species described worldwide (160,000), there are about 26,000 in Brazil (20.6% of the total). However, most species remain undescribed, and the global estimate for the number of lepidopteran species in the world is 500,000, and in Brazil, there are between 40,000 and 60,000 species yet to be described (35–57% of undescribed species still) (Heppner 1991; Brown and Freitas 1999; Kristensen et al. 2007). Doz-

I. R. Diniz (✉)
Universidade de Brasília, Brasília, DF, Brazil
e-mail: irdiniz@unb.br

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_17

ens of lepidopteran species per year are described in Brazil, but with a focus on the families of larger moths. This has not been mirrored by descriptions of small moths, or "microlepidoptera," which account for the majority of lepidopteran families. How many centuries of work would we need to adequately describe this fauna? Perhaps a focus on new species descriptions is not the way to work with such high diversity.

Brazil does not have centuries of lepidoteran research history, and very little was known about this fauna before Portuguese colonization in 1500. Scientific societies have an even shallower history—for example, the Brazilian Society of Zoology and Brazilian Society of Entomology were created less than 40 years ago. Nevertheless, the modern approach to studying ecological interactions is not new in Brazil; it started as detailed natural history studies without the sophisticated statistical analyses utilized today. Most notably, a very important natural history book was published by Angelo Moreira da Costa Lima in 1936 called, *Catalog of the insects that live on plants in Brazil.* An expanded edition was published 27 years later (1967) and included seven authors led by d'Araújo e Silva. Costa Lima also published a series of 12 volumes on the insects of Brazil, from 1939 to 1962, with two of these volumes dedicated to Lepidoptera. Naturalists such as Costa Lima, Lauro Travassos, Romualdo D'Almeida Ferreira, Ceslau Maria de Bienzanko, and Alfredo Rei do Rego Barros were leading researchers and dedicated their lives to the taxonomic study of the Lepidoptera in Brazil. Although these lepidopterists were serious about their work, there are plenty of humorous stories about their lives. Romualdo D'Almeida Ferreira, for example, had no university education and was a postman who collected butterflies in his spare time and then wrote taxonomic papers about his specimens in French and German so that he could publish them in France, Belgium, and Germany. His important contributions were ignored until he met Lauro Travassos, who recognized his incredible contributions to Brazilian Lepidoptera and gave him a job "delivering mail" at the Oswaldo Cruz Institute. Ferreira was the most prolific postman at the institute in terms of publishing on Lepidoptera, and he was probably the only one who never delivered a single letter.

There are many examples of foreigners who visited Brazil and contributed to great advances in Brazilian Lepidoptera. Julius Arp (1858–1945), from Germany, came to Brazil and worked in the textile industry in the states of Santa Catarina and Rio de Janeiro. He married a Brazilian woman and became a naturalized Brazilian in 1920. From an early age, Arp became a passionate lepidopterist, and over the course of 50 years, he formed an important private collection of South American Lepidoptera that included over 25,000 specimens (www.obrasraras.museunacional) and that was donated to the National Museum of Rio de Janeiro (MURJ). *Fritz Plaumann* worked for 70 years in Brazil; he came to Brazil from East Prussia (now Lithuania) with his family in 1924 after the First World War. Plaumann was an amateur insect collector and focused mostly on Coleoptera (beetles), Hymenoptera (wasps and ants), and Lepidoptera. The painstaking work of this self-taught researcher won the recognition of scientists around the world, and he has been honored by entomologists who have named over 150 species after him, most of which are beetles. Plaumann also put together a collection of Lepidoptera that now belongs to the Department of Entomology of the National Federal University of Rio de Janeiro

Museum (UFRJ). This is an important scientific collection, and it includes types, rare specimens, and endangered species, including *Dasyophtalma vertebralis* Butler 1869, which is considered extinct. In the 1970s, Plaumann was persecuted by the Brazilian Institute of Forest Development and was accused of "decimating wildlife" because he had sent insect specimens abroad due to his partnerships with museums in 12 different countries, including the British Museum, London, and Stockholm, Vienna, and Belgrade.

As I have already mentioned, I will not tell the story of all important Brazilian lepidopterists, but others that are worth mentioning include Ceslau Mario Biezanko, Henry Richard Pearson, José Oiticica Filho, Rego Barros, Luiz Soledad Otero, Mirna Martins Casagrande, and Olaf Hermann Hendrick Mielke. All of these lepidopterists have a colorful and interesting history and have contributed to our general knowledge of the systematics, ecology, and evolution of the order.

Contemporary Brazilian lepidopterists are an interesting group of researchers, and many are good friends. A great lepidopterist and a very dear friend is Vitor Osmar Becker. His parents were small farmers in Brusque (Santa Catarina) in southern Brazil. He is married to Clemira Souza and has two sons: Apoena (named after an indigenous chief), Rubiara (the one who believes), and a daughter, Moema (extroverted or the flower that opens in the morning); none of them became lepidopterists. Vitor has always been a lover of nature, especially insects. He earned a BS in agronomy and forestry at the Federal Rural University of Rio Grande do Sul in 1967, an MS in forestry at the American Institute of Agricultural Sciences of La Organización Los American States (1973), and a PhD in entomology at Imperial College (1981). After finishing his doctorate, Vitor has focused his entire academic career on studies of Lepidoptera, under the initial influence of Bienzanko, and is a well-known lepidopterist, with over a hundred published articles. Vitor created and curates one of the largest collections of Neotropical Lepidoptera in the world, which is an important part of the Uiraçu Research Center that he directs. This collection contains more than 300,000 specimens, representing more than 35,000 species, which ranks it third for Neotropical Lepidoptera, after the Natural History Museums in Washington and London.

Over the course of doing extensive fieldwork in Latin America, Vitor watched the rapid and drastic destruction of natural habitats and decided that it was pointless to continue collecting and preparing material to include in collections while doing nothing to preserve the species in the wild. Vitor and Clemira worked for years on plans for preserving threatened habitats for conservation, research, and environmental education, and when Vitor retired as a researcher at the Brazilian Ministry of Agriculture (EMBRAPA) in 1997, he and Clemira dedicated their efforts towards conservation of a remaining fragment of Atlantic forest in Bahia, Brazil. The Atlantic Forest is not only one of the most diverse biomes in the world but is also one of the most deforested in Brazil, and today there remains less than 8 % of the original forest. In 1998, Vitor and Clemira established a reserve, Serra Bonita, to preserve a portion of this high-biodiversity ecosystem. To help manage this reserve, the Uiraçu Institute was established as an NGO, and the total protected area is now 5000 acres and includes a research center with laboratories, housing, collections, an auditorium, a library, and 10 km of trails.

Vitor is a grand storyteller, and it is difficult to rely only on his anecdotes, but the story that captures his persona the best is as follows. Vitor was driving on a family-collecting trip with Clemira and their very young baby. Vitor stopped to collect some rare moths and then handed the envelopes containing the specimens to Clemira, who was in the car with the baby, diapers, pacifiers, and other essentials. She immediately dropped the envelopes, and Vitor became very agitated, asking why she was not more careful with such valuable specimens. She answered, “I was occupied with nursing our baby and had to make sure he did not fall.” He then said, without pause, “You could have let the baby fall, because we could easily make another one of those, but I may never see these species of moths again.”

Another colorful Brazilian lepidopterist is Keith Spalding Brown Junior, who earned a PhD in organic chemistry at the University of Wisconsin, Madison, in 1962. He was a professor at the State University of Campinas (Unicamp) and a very productive scientist who studied chemical ecology, evolution, and butterfly systematics. He was the academic adviser of many important contemporary lepidopterists in Brazil, including Amabílio José Aires de Camargo, who is the curator of the entomological collection of Embrapa Cerrado (Agricultural Research Centre of the Cerrado-EMBRAPA). Camargo specializes in taxonomy, phylogeny, biology, ecology, and distribution of Saturniidae. Other contemporary Brazilian lepidopterists who could fill hundreds of pages in this book with fun stories and details of their important contributions include André Lucci Freitas, Cristiano Agra Iserhard, Danilo Bandini Ribeiro, Felipe Amorim, Gilson R. P. Moreira, Helena Piccoli Romanowski, Lucas Augusto Kaminski, Marcelo Duarte, Márcio Uehara-Prado, Márcio Zikán Cardoso, Onildo João Marini-Filho, Ronaldo Bastos Francini, and Viviane Ferro. This list includes systematists, evolutionary biologists, ecologists, and applied biologists who have contributed to studies of Lepidoptera as well as conservation, agriculture, and other applied issues.

As with other regions of the world, the immature stages of Lepidoptera (caterpillars) have never been the main focus of lepidopterists. In fact, very little is known about immatures of most described species of Brazilian Lepidoptera; this brings us to the research that I (Ivone Rezende Diniz) have done with Helena Castanheira de Morais, studying thousands of species of caterpillars in the Brazilian Cerrado. Our research with caterpillars was always in the Cerrado, which is a savannah-like biome with a pronounced dry season. The Cerrado forms a large corridor between the Amazon Forest and the Atlantic Forest. Helena and I live in Brasília (the capital of Brazil), which is the central region of the biome (see Fig. 17.1) and work at the University of Brasilia.

Here, I provide just a few details about our personal lives. I am married to a political scientist (Antonio Brussi), and we have three children: Daniel, who is a network engineer; Clarisse, who is a mammalogist; and Julia (Antonio’s daughter), who is an anthropologist. Helena never married and never had children but has a niece who is a limnologist. Over the past 25 years, we have been dedicated to the research of plant–caterpillar interactions. Since we stumbled upon caterpillar work

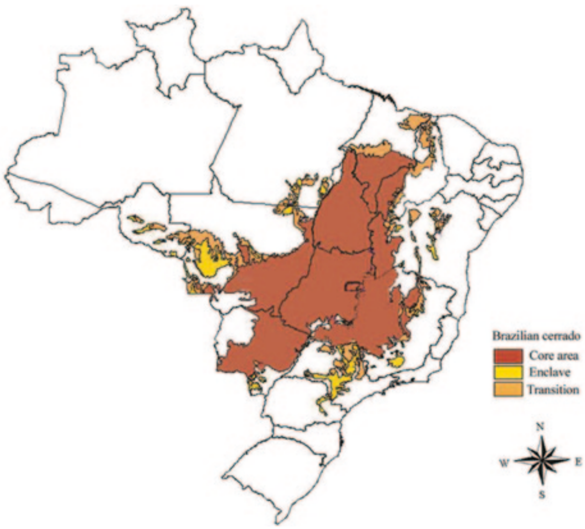


Fig. 17.1 Map of Brazil showing the localization of the Cerrado biome

and passion later in our careers, our history is different from many other lepidopterists, who have been passionate about butterflies or moths since childhood. For a short period, I had developed a research program on the ecology of solitary wasps, *Zeta argillacea*, directed by Anthony Raw, a hymenopterist who came to Brazil in 1997 from England to contribute to the ecology graduate program at the University of Brasilia and never returned to England. My interest in wasps continued until a maid asked me, could you not find anything more interesting to do? And upon reflection, I thought, “she is right, I will change my research focus.” After that, I had the opportunity to go to Edinburgh to study animal behavior, and I could not stand the bitter cold of that place, so out of pure convenience I chose to study behavior of insects—in the laboratory where it was warm. Which insect did I choose to study? The easiest to buy and maintain in the laboratory: cockroaches. The result of 2 years of work on the behavior of these insects was three published papers and a strong memory that still lasts today of the unbearable smell of the laboratory. Back in Brazil, where it was warm outside, I started to develop some projects examining insect communities in the Cerrado (Fig. 17.1). I focused on the effects of fire, which is naturally frequent in the Cerrado.

Helena always loved ants, so it was a natural research organism for her. She published very interesting articles on the effects of fire on ant communities and also on the foraging behavior of predatory species. The shift in our focus to the Lepidoptera came after Professor Peter Price visited the University of Brasilia in the early 1990s. Both of us were always inviting scientists like Price to visit and get to know the Cerrado, which covers 22 % of the country and is a biodiversity hotspot. Besides having a great admiration for Price’s research, we were also taken by his kindness and generosity. When he visited the Cerrado, he was very curious and full of questions, especially questions about the herbivores, such as the following: What are the most common herbivores that consume the cerrado plants? Are there more generalists or specialists? At that point, we realized that there is almost nothing known about the cerrado herbivores, and we decided to answer some of Price's questions by focusing on the most important herbivore in many terrestrial ecosystems: caterpillars. If Peter Price returns to Brasilia again, we are now ready with some answers. For example, we were coauthors of the first lists (in 1995 and 2002) of cerrado caterpillars and their host plants, so we now know many of the herbivores of the Cerrado. After 25 years of collecting and rearing caterpillars, we do not have answers to all of Price's questions, but everything that is known about trophic interactions involving cerrado caterpillars is almost entirely based on our data. Despite all the difficulties associated with rearing Lepidoptera and the small number of researchers dedicated to this endeavor, we hope that new researchers will continue this work. The cerrado caterpillar experts of the future include Cintia Lepesqueur, Laura Braga, Neuza Aparecida Silva, and Scheila Scherrer.

Thus, decades of collecting and rearing caterpillars all began with some simple questions from Peter Price, making us realize the importance of these types of visits. Today, we are still dedicated to studying caterpillars and their trophic interactions, and this work has brought other fun lepidopterists to the Cerrado, with whom we have become friends, including Robert Marquis (University of Missouri) and Lee Dyer (University of Nevada), who currently visits twice every year. These lepidopterist visits were and still are important to us, to the University of Brasilia, and to our students.

There is so much we can say now with certainty about cerrado caterpillars and their interactions with other organisms. The long dry season in the Cerrado that can last up to 6 months with almost no rainfall and with very low relative air humidity means that we have two very specific communities of caterpillars. Normally, the abundance of larvae per plant is very low, and locally, there are more specialists than generalists. Caterpillar species' richness reaches 50 for some host plants, such as *Roupala montana* (Proteaceae). The caterpillars are more abundant in the dry season, especially in the first half of the season (April to June). Based on 10 years of collecting, there is strong seasonality of caterpillars in the Cerrado (Fig. 17.2; Gray = dry season). The composition of caterpillar species changes by around 80 % between the dry and rainy seasons in the Cerrado (Fig. 17.4). Beyond some of these strong patterns, there is still a huge unknown world of trophic interactions to be revealed in the Cerrado, including the wet gallery forests that form along waterways and have not been studied.

Even after 25 years of work in the field with Lepidoptera, I have never gotten over my poor skills at spatial orientation, and I must always pay close attention because I get lost easily in the Cerrado. But I still go out there. Helena is retired now and is dedicated to the loom, weaving carpets and bedspreads (Fig. 17.3). I tried to retire a few years ago because I would also like to try to be a seamstress and designer. But the caterpillars do not leave me alone, so for now it is a dream that I could someday do some work related to women's fashion. Even worse, I now have a pile of extra work at a Brazilian funding agency… that for now, I do not want to think about!

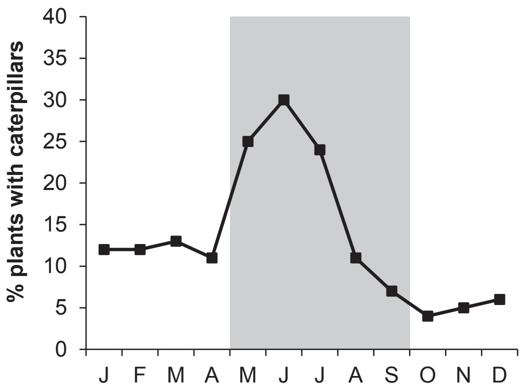


Fig. 17.2 Higher abundance of caterpillars in the dry season. (Morais and Diniz 1999)

Fig. 17.3 *Left:* Helena Castanheira de Morais, and some students. *Middle:* Neuza Silva, Laura Braga, Ivone Diniz, and Scheila Scherrer (all lepidopterists). *Right:* Ivone Diniz, Neuza Silva, and Cíntia Lepesqueur on the day of the release of the book on Cerrado caterpillars

Fig. 17.4 Some caterpillars collected in the Cerrado. Top panel: *Battus polydamas, Eustema opaca.* Bottom panel: *Phobetron hipparchia, Kolana ergina, Leucanella memusae.*

Acknowledgements My sincere thanks to Lee Dyer for the invitation to participate in this book, and for the extraordinary translation of this chapter. Thanks also to Cynthia Lepesqueur and Neuza Aparecida Silva for providing some images presented in this chapter.

References

Brown KS Jr, Freitas AVL (1999) Lepidoptera. In: Brandão CRF, Cancello EM, Joly CA, Bicudo CEM (eds) Biodiversidade do Estado de São Paulo, Brasil: Síntese do Conhecimento ao Final do Século XX. 5. Invertebrados terrestres. FAPESP, São Paulo, 279 p, pp 225–243

Heppner JB (1991) Faunal regions and the diversity of Lepidoptera. Trop Lepidoptera 2:1–85

Kristensen NP, Scoble MJ, Karsholt O (2007) Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa 1668:699–747

Morais HC, Diniz IR (1999) Caterpillar seasonality in central Brazilian cerrado. Revista de Biología Tropical 47:1025–1033

Ivone Rezende Diniz is a full time professor at the Universidade de Brasília in Federal District, Brasília, Brazil, where she has taught entomology and ecology since 1977. She received an M Phil from the University of Edinburgh, and her doctoral degree from the Universidade de Brasília. Her current research focuses on immature stages of Lepidoptera and their interactions with plants in the Cerrado biome (a savanna-like vegetation) in Brazil. During her free time, which is not much, she enjoys reading, dancing, gardening, cooking for her family and friends, and having nice meals accompanied by a good red wine.

Chapter 18
Butterflies on a Dragon's Head; Butterflies in a Dragon's Head[1]

Roger L. H. Dennis

When Matt and Lee asked me to contribute to this book, I was, at first, bemused by the invitation. Glancing down the familiar list of authors, I was immediately struck by the fact that I was the only lifelong amateur and, very likely, the only one who had missed out completely on school biology (it wasn't taught then in our arcane institution on the isolated Welsh borderlands). I hadn't collected butterflies as a hobby, and my PhD was not in butterfly science but on a rather limited aspect (dermatoglyphics)[2] of those distinctly destructive critters: humans. Even now, my entomology lab experience is sparse; no butterfly biology students can claim I ruined their careers, and nose-to-ground fieldwork was abruptly terminated early on in my mid-thirties: any lepidopterist will tell you that is a real killer. I could boast a distinction—perhaps an appalling one for an entomologist—that my butterfly books have the least possible number of plates of set butterflies in them. In my defence, I would retort that I like my animals alive! Anyway, along with the other contributors, and armed with some suitably inspiring homework from Art Shapiro (William Leach's *Butterfly People*), I offer some personal recollections before they deliquesce into larval soup.

One thing I do suspect may link many of us: Some early event triggered a lifelong attachment to Lepidoptera. I have been thinking about butterflies most of my adult life; that seems natural to me, but it must register as being distinctly eccentric to most humankind. Herein I touch briefly, in an imbrication of events, on the stimuli that tooled this strange path, especially on the very first study from which all else grew, and the consequences—well, some of them. Just what tracks our different courses have taken among butterflies is almost certainly bound up with the vagaries

[1] Dragon's Head refers here to two dragons; the first is the Viking named Orme's Head (Dragon's Head), the second is a conundrum (Bickerton is a window of opportunity).

[2] Human palm and finger prints (Dennis 1977a). See Cummins and Midlo (1961).

R. L. H. Dennis (✉)
Institute for Environment, Sustainability and Regeneration, Staffordshire University, UK
e-mail: rlhdennis@aol.com

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_18

of serendipity and, its converse, zemblanity:[3] A lesson, if it need be taught at all, is that the latter can, counter intuitively, lead to good things! But, perhaps my first stop should be to claim an inheritance, for the suggestible among you perhaps even a reincarnation: A month after an entomological uncle died, I appeared apparently determined to stick to butterflies rather than dealing with much nastier insects he mastered—mosquitoes, midges, and flies. He was my father's mother's brother, J. W. S. (Jack) Macfie, and a far better entomologist than I would ever have been[4]; he even has a mosquito named after him *(Culex macfiei)*, lucky chap! I knew nothing of him other than as the author of a rather tortuous monograph (taxonomy) on family history, in which a limited selection of first names is repeated, frustratingly, through the generations. In complete surprise, he came to my attention on my father's brother's death in 1983, more than a decade after my own interest had developed. The family lived a short distance from us here in Wilmslow, Cheshire, at Rowton Hall, Chester; as an 8-year-old he had caught a migratory Long-tailed Blue at Heswall, a rarity in the UK, the first record for the county.[5] Recently, he has appeared in a tribute in *Antenna* by an Australian entomologist D. S. Kettle; he volunteered (concealing his real age) to serve with the British forces in his 60s as a major (malariologist) to assess the healthiness of potential landing drops for British troops in Africa and the Near East in World War II[6]. Apparently he hated formalities and being saluted and told the then subordinate noncommissioned officer (NCO), who became a distinguished entomologist in his own right: 'Don't do that to me.' That's the kind of eccentric stock I come from. So much for inheritance; you can believe what you like.

Now what of those random events? Well, the first impression on a young Dennis of a winged creature was, in fact, man-made—of a tall man sitting in a cockpit of a Spitfire V in a framed photograph over the fireplace. This was soon overtaken by a bird. One day, when I was three, the gardener brought down a carrion crow's egg from a high nest, made two crude holes in either end, blew out its life, and gave it to me; a brief event admittedly, but thereafter my senses were hooked to the natural world: sight, smell, and touch, and you are captivated by it. I may have stayed with birds and never have started on butterflies but for the mangled Spitfire pilot—bust up during the war, he bust himself up again at the war's end in a spectacular fashion in a post-dinner car crash returning home to Oakley from Erddig.[7] Brain-damaged and broken by his 30th birthday, we limped off to South Devon from Shropshire. Before travelling south, we first stopped over at Shropshire's Hawkstone Park. It was here I saw my first moth, a rather stunning emerald micro, *Tortrix viridana*. My mother impressed me with her philosophy (names were unimportant, the essence was experience) if not her knowledge.

[3] From Boyd 1998.

[4] Mattingley 1949.

[5] Pierce 1892.

[6] Kettle 2000.

[7] Erddig Hall, landed seat of the ancient Yorke family (http://www.nationaltrust.org.uk/erddig/history/). Oakley Hall, seat of Chetwode family since the thirteenth century, is near Market Drayton, on the border of Shropshire and Staffordshire.

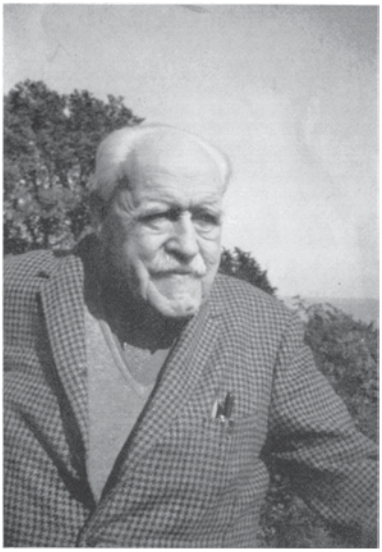


Fig. 18.1 Frank Henry Lees, one of Britain's most successful lepidopterists. (Courtesy of Colin Plant and *Entomologist's Record*)

On arriving in Devon, our first stop was a rented bungalow at Maidencombe—one of three in a cul-de-sac, on a steep hill. Our next door neighbour just happened to be Frank Lees (Fig. 18.1); as I discovered later from his obituary,[8] he was known for recording the first of a number of rare migrant moths to Britain: His trap was as a 'lighthouse' facing the English Channel. His magnificent collection went to Exeter University. He had spent his long retirement collecting and breeding moths, and a chance meeting—owing to an innocent act of trespass in his garden—resulted in a conducted tour of his collection, an initiation into lepidopterology, and a present:

> The summer began to slip away to early autumn tints. Unripe fruit hung from laden apple trees; small hard pears lay aborted on the ground and eager wasps bit at their sugars. By now I often wandered along the lane above the bungalow on my own, touching the fruit and trunks of trees, exploring textures and shapes. For some time I had noticed that the branches of trees in the garden of the adjoining bungalow had grown bags as well as fruit, bags of net curtains; some were low down within my reach and I trespassed to inspect them closely, pressing the bags to my face. Their necks were tied in place; inside them, I observed crawling creatures, mobile twigs, whose every move was a comically acute genuflexion. I had little time for further exploration when my left ear was gently but firmly tugged. 'Now what are you doing; this is not your garden, is it?' I had a problem with the concept of ownership and simply looked up at him as best I could thus impaired. He was an old man with hooded eyes, a long chin and a neatly groomed white beard; he was dressed formally in a heavy tweed jacket and smelt of moth balls and some other sweeter poison. He had a pleasant face that belied his stern greeting, a gentle voice, and we walked back to our bungalow, he with his hand lightly on my shoulder. When home, he rang the bell and my mother appeared. 'Mrs Dennis', he said, 'I am Mr Lees, Mr Frank Lees, your neighbour. I found your boy wandering about my front garden inspecting my larval sleeves.' My mother looked puzzled but unconcerned. He went on: 'I think I can show him better things to do than wandering aimlessly about other people's property.' Mother then understood and was all apologies. Suddenly, his manner softened: 'If you like, I can show him what those caterpillars in the nets turn into', he added with a twinkle, and winked at me. I must have looked, because I

[8] de Worms 1974.

felt, distinctly intrigued; did the creepy crawly things actually turn into something else or had I misheard him? Mother was all acquiescence and we started back to his house.

‘I have caterpillars in these nets. One day, they will turn into moths. Now, would you like to see some moths?’ I nodded enthusiastically and we dropped down the path past the bungalow to the back garden. He was slow and stooped; oblivious then, years later I understood: he was an old man about to pass on something very precious, the baton of his life’s devotion. The back garden had a patio and on it was placed a round container with a pear shaped light bulb inserted between metal vanes. ‘One of my moth traps; they come to the light.’ He gestured with a hand. We entered the back door up a narrow path overhung with dripping purple and scarlet fuchsias—I was sorely tempted to reach out to them—and were greeted by his elderly sister. He opened a book case to the left of the door. ‘Let me show you something first.’ He picked a book off the shelf. Years later, I recognised it as South’s ‘British Moths’. He opened the book at a colourful plate and gently introduced me to the world of Lepidoptera. I was astounded. ‘Would not it be nice if we too could turn into creatures as beautiful as moths? Now, let me show you something rather special.’ We mounted the stairs to a large dormer room; we were immediately enveloped by the aroma of those enticing poisons and becalmed in camphor. Inside was a large solid table near the inner wall; around the edges were an array of cabinets, Hill units, on the other three sides. I have a strange memory of another moth trap bayonet-fitted into a round hole in the rear wall above and to the right of the window, a light house to crumbling cliffs at the edge of the Atlantic Ocean. The table had setting boards, pins, a microscope and other equipment neatly arranged on it. He moved to the far wall and took off the doors to several of the units. Then, as if by magic, he opened drawers to a palpable Heaven. Under glass, lay rows and rows, neat lines of set butterflies and moths; an array of unbelievable creatures contrasting in size, shape, colour and pattern met my eyes. In disbelief and wonder I stared at them. He pointed as he ran through names as exotic as the creatures themselves: ‘Privet Hawk, Eyed Hawk, Death’s Head Hawk—look at the skull—Rosy Footman, Purple Emperor, Swallowtail, Clouded Yellow.’ The list ran on and on and, entranced, I consumed names and visions as greedily as a young Turk. There were tiny ones too and it was impossible to see how they could have been set so immaculately. Eventually, as any child might, I blurted out: ‘What… what, will you do with them when you go to Heaven?’ My mother and Mr Lees looked at each other and laughed. He knew he had a convert to the world of natural history. My life had begun and in some way his life was instantaneously fulfilled: the transmission of that special intelligence, a deep love of nature, had been achieved.

In days to come, I watched the butterflies orbit his buddleias, and at night cascades of moths fell like doomed stars into the galactic black hole of his purple U/V garden trap. I had Privet Hawks and Garden Tigers run over my hands, and everything in me screamed with delight. But, even at this age I found something sad about their fragile beauty which could only be maintained by spreading them out on open boards, as shot crows strung out on a barbed-wire fence; it was as if we were repeatedly nailing Christ to the cross. In my late teens, after this interest was for a second time fired and bit deeply, I soon freed myself of this innate materialism and was happy only to study them alive. Whatever the cause, for science as for pleasure, it wounded me to see them killed; it took a little time, but with the end of it came relief. Anyway, my period of freedom was short-lived; the September before my fifth birthday I was sent away to boarding school; not far, but a few miles away at Torquay’s Winchester Lodge. But, for a little boy it might as well have been light years away. In my hands I had two presents from Mr Lees: an old oblong box with a close fitting lid full of fragile winged gems, and a cage inside which was a hungry Pipistrelle bat. Needless to say, I was soon relieved of them, as of all sentience, on arriving at my first school—to this child, and to many others, a prison sentence in a torture chamber. There was one last pleasure as the bat escaped and spun round the dormitory to consternation of staff and the delight of fellow inmates. For many years visions of the specimens in that box would remind me of Clouded Yellows and Marbled Whites on the downs that plunged to the Devon cliffs and of that most delicate verdant filigree on the closed wings of an Orange Tip.[9]

[9] From *Mae’r hafan casáu*. Unpublished work.

A third incident in serendipity is not a comfortable one to unwrap, bound up as it is with its polar extreme. A few words must here suffice for veiled turbulent events, a web of incongruities, which at face value must seem as an anomalous, callous detachment: I was 11 years of age, my brother 8; father had just committed suicide, and mother was by now a broken alcoholic. Yet…we felt the luckiest boys alive: We were free. Free to roam when and where we wished over the Welsh borderlands, where we had by now moved. On returning home for the first long vacation, mother rocked unsteadily on the top garden step and, with one of those grand gestures borrowed from the Hollywood greats, bestowed on us all the woods and hills around: We grabbed the opportunity with relish and lived like feral animals—out at dawn and back after dusk often to an empty house—eating off the land and from friends' tables, until the bell rang in a new prison term at the next institutional oubliette for mental compression and containment. I said I had no formal biology teaching prior to undergraduate level; instead, we learnt our ecology on the hoof and developed an intimate knowledge of the habits of local birds and animals. My brother—as yet untutored in the surgical arts—dissected owl pellets and mammal cadavers on the kitchen table and collected lizards and dragonflies (Tim is the real zoologist, a Cambridge vet; you have to bust a gut to achieve that—the failures, he tells me, became medics!). It was his hamsters that gnawed their way through the sides of our school trunks and whose pigeons buried the garage floor in a glutinous accretion of guano, though I have to admit it was my old pheasant hanging from the kitchen ceiling whose feathers fluttered loosely about, like autumn leaves, and from whose rotting corpse spawned a plague of bluebottles! These, and other events, were light moments in a long period of raw experience from which we sought an escape in the borderland wilderness. To butterfly people, it is perhaps a heresy to admit that there is nothing to match a dawn chorus on a May morning in an English country garden, but that is the way of it. When I met butterflies again, instinctively, I knew what they were all about too.

That moment came some years later in my last days at my Welsh Marches school, whose history enveloped uncompromising rituals so arcane that—at its inception—the USA was not yet a twinkle in the eye of its first European settlers, let alone its founding fathers. It was a simple act, repeated endlessly by all boys at that time without electronic devices to distract them, of slipping a book down off a library shelf; it was one newly catalogued I had not seen before. It was the unmatchable E. B. Ford's *Butterflies*[10] (Fig. 18.2). No matter that I had missed out on biology; here, as I was preparing to head to Durham University to read anthropology and geography, was all the butterfly biology anyone needed. It is simply a delicious text—yes, illustrated with thought-provoking colour photographs—laden with fascinating topics, each inspiring inquiry. I still have my own copy (a geography prize!) stuffed with index cards of scribbled notes, the margins desecrated—I admit to my shame—with my immature acerbic comments. Many (any!) of the chapters were enough to propel a new interest; but, one in particular—the last—galvanised my attention. It did so because I came to it from physical geography and geology, not from biology. Antagonised by institutional pedagogy to a state of desperation by this stage, I had taken over my own education. It could only happen in a British minor public school under

[10] Ford 1945.

Fig. 18.2 Images of Professor E. B. Ford (from the dedication in Vane-Wright R. I. and Ackery P. R. (1984) *The Biology of Butterflies*. Symposium of the Royal Entomological Society No. 11. London: Academic Press) and of his two most popular books, *Butterflies* (1945) *(lower right* and *left)* and *Moths* (1955) *(upper right)*, London: Collins New Naturalist Series

a new liberal head who had the sense to realise the school's limitations and the best way to keep a Dennis occupied. 'A'-level geography—for university entry—I had consumed at 13 in a third form frenzy of fascination, and thereafter I ignored all else (home then was arguably the most geologically diverse part of England).

This last chapter in Ford's book is, of course, on *The Origins of Butterflies;* immediately, I could sense some pending intellectual *lapsus*—a large fraction of the fauna was regarded as surviving the last major glaciation, in situ, on British soil; overwhelmed as if by a tsunami of ideas and instincts, I puffed about the school the next few days with that sort of righteous indignation only the very young, inexperienced and evangelically dismissive can display; could an Oxford professor be so wrong, I puzzled. In fact, could other eminent intellectuals cited in the book, like Bryan P. Beirne and J. W. Heslop-Harrison, distinguished titans of the entomology world, also be wrong? Of course, I soon learnt that human infallibility has powerful tendrils even into the upper echelons of academia and, in any case, it has long been a dogged companion! Still, just a decade later, with the arrival of my first reviews, all but one compliant—the exception, a rasping diatribe on delivery rather than content—I would have communicated less euphuistically to what I saw then as the gangue-filled fault lines running through those pages in Ford's *Origins*. Even so, from my current weather-beaten vantage, I can feel decidedly uncomfortable for my predecessors with a harebrained 6th former on the loose.

The last piece in this jigsaw was our move to North Wales in search of a healthier location on the coast. On our arrival at Rhos in 1966, the Little Orme's Head lay directly ahead of us shimmering in bright sunshine along an avenue of spring blossom; the Great Orme's Head (Worm or Dragon's Head[1]) barely concealed by the prominent limestone ridge of Nant-y-Gamar. It was an extraordinary opportunity—all brought about by family misfortune—to land on what was to become recognised as one of Britain's butterfly hot spots. Much of our time was spent on the cliffs, taking photographs of birds' nesting sites; occasionally, I am still jolted awake at night by visions of our narrow scrapes, particularly, my brother's fall from a 100-ft cliff. From here, during the next year, I would traipse across Germany and Norway on school trips, on my own in Scotland (based at Kindrogen Lodge Field Centre) and Snowdonia, to study glaciated landscapes. At home, I had the fossil Holocene[11] forest on Rhos beach to contemplate, the till cliff exposures on the Little Orme and the mollusc-laden tufa and solifluction benches on the Great Orme, all before seeing Ford's book.

The revelation, such was it to me, in that important chapter, was simply that something as fragile as the temperate butterflies of meadows and woods could be thought to survive the onslaught of a glaciation; even our Neanderthal cousins would have been seriously challenged by such refrigeration! Gradually, it dawned that previous reconstructions, so boldly articulated, had been based on a limited set of unsupported assumptions. First, the northwest races (subspecies)[12] of British butterflies, distinguished by wing patterns from those of southern England, were attributed great antiquity. Second, dispersal capacity in butterflies that were not blatantly migratory was assumed to be very limited indeed—waterbodies as extensive as the English Channel were thought to impose complete barriers—and movement for most butterflies was considered to require land bridges or at least narrow sea straits that could be hopped across. The deduction was that the Irish fauna and British subspecies had evolved in situ on glacial refuges within, or offshore of, the British landmass. The account of the Pleistocene juggernaut in these early reconstructions by my predecessors—of ice, sea levels and climate—was admittedly distinctly sketchy and the potential impact greatly underestimated. It was no fault of Ford, or Beirne or Heslop-Harrison, of course; the orthodox view of glacial refuges was still that of Forbes from the 1840s, and anyway, things had moved on swiftly in geomorphology between their publications and my reading them (though they hit me as fresh as columns in that day's 'Times'), and no one else had blundered into the hiatus. Then, there was no 'Health and Safety', no cautionary hand on a shoulder; 1960s 6th formers had no mentors and sought none, university students were summarily thwarted by lecturers with 'FOFO' (a translation is unprintable!), and I fell headlong into the subject but through sheer good fortune landed on my feet.

The punch line I had read, and found increasingly difficult to accept, was that many British butterflies had evolved in response to glacial conditions, in situ, in British refuges. But, where—and when—these refuges were speculated to occur must have existed massive ice caps, sea, severe permafrost and a run of such appalling 'summer' weather that would have compelled an instantaneous Inuvik-type construction of covered courts over the whole of Wimbledon. Certainly,

---

[11] Holocene (Postglacial; postdating 11,700 BP to the present) is the latest epoch of the Quaternary and postdates the Pleistocene (dating from c 2.59 m BP), the most recent epoch of repeated glaciations on the planet.

[12] A subspecies is a distinct subdivision of a species, usually a geographically isolated population(s). See Mayr (1963).

many organisms (plants, vertebrates and arthropods) will have survived in tundra isolates, but for thermally challenged temperate butterflies to have done so seemed highly unlikely. If they had survived the last great glaciation (Devensian, 20 ka BP),[13] then why not all of the ice advances, and, again how many glaciations had there been? At that time, it was considered just four, now the number is known to run into double figures. My own view was that one or both of two alternative paths could have been adopted by the distinctive-looking subspecies: Either they had evolved elsewhere (i.e. Europe, south of the Alpine chain), subsequently entering in the wake of the ice, or they had evolved near enough in situ but later—after the ice and in very different conditions—at what appeared to be hugely faster rates than supposed. This is not the place to cover that ground again; the fallout of ideas and facts is too vast a subject to cover here; suffice it to say the work is still ongoing and future generations of lepidopterists, charged with molecular data and a finer geological record still, will close down on outstanding riddles and sift out the alternatives for each clade[14]. My reconstruction, in turn, will then appear to be archaic; if not, then we have not progressed. It is enough here to point to the swing in understanding: refuges further away in Southern Europe, rapid movements of plants and animals, similarly swift transformations of populations—their genotypes and phenotypes—all in response to sudden shifts of Quaternary and current climate changes and environments.

The immediate question in 1968, however, was how best to test something one couldn't palpably clasp in fossil evidence! It was here that the Great Orme and North Wales paved the way. Two of the butterfly races attributed to glacial refuges and evolution by Bryan Beirne occurred on the Great Orme's Head (Fig. 18.3), an azure blue *Plebejus argus caernensis* (Fig. 18.4) and a mottled brown *Hipparchia semele thyone* (Fig. 18.4). Ford, with his long experience in genetics, differed in view and pointed to possible limited gene effects and Holocene evolution, though confusingly (on the basis of its occurrence in Ireland) he placed the Grayling *H. semele* with Devensian survivors in the UK. Both 'races' had been described by J. Antony Thompson in the 1940s, and Ford had usefully repeated the details in his text. Fascinatingly, though unrelated species, both are dwarf races whose adults emerge earlier than populations elsewhere in the UK; they also have unusual wing patterns. A vital point of further interest is that the blue had been transferred by A. J. Merchant[15] (1956) during 1942 (90 individuals) to a single slope of a matching biotope on Carboniferous limestone some 13 km eastwards in the Dulas Valley. Several ideas could be immediately tested. Had the phenotypes (appearance) of

[13] The last glaciation c 20,000 years ago is given different names in different regions, viz., Fraser (in the Pacific Cordillera of North America), Pinedale (in the Central Rocky Mountains), Wisconsinan or Wisconsin (in central North America), Devensian (in the British Isles), Würm (in the Alps), Weichselian or Vistulian (in Northern Europe and northern Central Europe), and Otira in New Zealand.

[14] A clade is a group consisting of an ancestor and all its descendants, a single 'branch' on the 'tree of life'. A clade is by definition monophyletic, meaning it contains one ancestor (which can be an organism, a population or a species) and all its descendants. See Huxley (1957).

[15] Merchant 1956.

Fig. 18.3 Satellite image of the Great Orme's Head in North Wales and a view along the western scars of the Great Orme's Head from the south (2005)

the two races remained much the same after little more than just 20 years—was that sufficient time for populations to become distinct? Had the Dulas valley blues extended their range across the open farmland to the other side of the Dulas Valley? Did they still look the same as their founder population? How different were these 'races' from other populations in North Wales? On top of these issues, other questions also surfaced. Just how were the two species distributed over the Orme, and was the population uniform throughout the flight season?

These last two questions, and others, became evident as a string of lepidopterists turned up at our door in Rhos seeking the whereabouts of the Great Orme's treasures; among the exotic, one retired accountant appeared with his (third) young wife in a spanking new Rolls Royce trailing a large caravan; apparently, she chased after the quarry while he, too volumetrically challenged for such extravagant exercise, dealt with the victims using an arsenal of killing bottles arranged neatly in milk trays. Rumour had it that the turnover in wives related to wear and tear in the chase! I directed him to the most precipitous and coldest of slopes. It is too long ago now to recall all the strange and interesting characters who came to our door; I can only say they gave my mother endless amusement and entertainment, and she clinked glasses with many of them, treating them to her husky-voiced, Hepburn performance while puffing nicotine doughnuts in their faces.

Fig. 18.4 The Silver-studded Blue *(Plebejus argus caernensis; top)* and Grayling *(Hipparchia semele thyone; bottom),* both males, on the Great Orme's Head

In 1968 I started obtaining equipment from Watkins and Doncaster, though my net through that first season was still a coat hanger draped with a net curtain! I had also started to subscribe to the *Entomologist's Record;* my appalling first 'paper' (should that be—my first appalling paper!), a jargon-laden description of *thyone,* was sent off in 1969. The study started in earnest after a visit by Peter Crow, a knowledgeable amateur entomologist about to retire to the Welsh mountains. He paved my access to the Royal Entomological Society Library, to articles which otherwise would have been impossible to track down (no simple web searches then). I had previously met Hugh Michaelis (Fig. 18.5), who lived nearby at Glan Conwy; his knowledge of Lepidoptera I have found to this day unsurpassed, and his quiet and thoughtful kindness was all one would expect of an Old Mancunian; he introduced me to the coast-hugging *Lycia zonaria* and its flightless females on Conwy Morfa's beach—another piece in the postglacial evolutionary jigsaw puzzle. Now, if I start on a detailed account of what transpired, this will become a rather tedious monograph.[16] A glimpse of what emerged then: These butterflies were distinct but

[16] Dennis 1971.

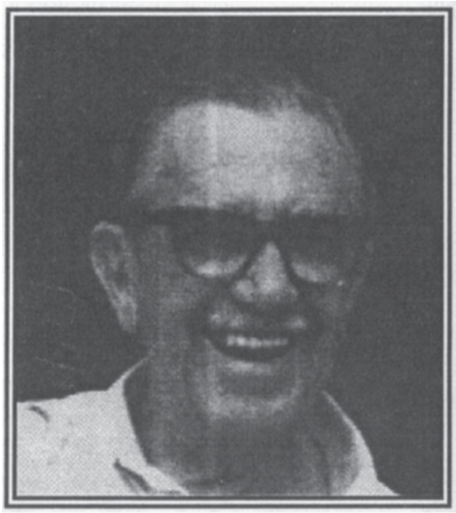


Fig. 18.5 Hugh Michaelis, a highly gifted North Wales lepidopterist and specialist on Microlepidoptera. (Courtesy of Richard Underwood of the Raven Society)

could not have survived the Devensian tabula rasa in Britain.[17] The 'races' had evolved in the current interglacial (Holocene) and are almost certainly adapted to the unusual climate (wind blasted, desiccated and sun drenched) and substrates (toasted, thin rendzinas over pervious and precipitous limestone) of the Orme, effectively an island, particularly the west and south aspects. Moreover, wing patterns could change significantly and amazingly quickly, as had the blue on the Orme and in the Dulas Valley. Even the Silver-studded Blue could move—it had crossed the valley without a convenient corridor−and the speed demonstrated by the Grayling suggested it could easily outpace Roger Bannister and hurdle barriers like Ed Moses. A clear gene effect for the race was discovered in the Grayling; a population of the butterfly that had colonised the adjoining dunes in the Conwy estuary from the Orme remained effectively dwarfed, and the protracted Orme population got significantly bigger as the season progressed, indicating reciprocal movements from the Conwy and Deganwy dunes and a substantial degree of temporal isolation between earlier and later eclosions.

The scene was set for rethinking the origins of the entire British butterfly fauna. Initially, I tried to obtain a PhD studentship to follow up all these ideas from the Orme's Head and the larger peninsula of which it formed a part, the Creuddyn. Durham said they could find no one qualified to supervise the work.[18] I tried further

[17] In an e-mail from a colleague Dr Leonardo Dapporto on 21 September 2014, it was confirmed that the distinction of *H. semele thyone* is not at species level, the butterfly having the same deoxyribonucleic acid (DNA) COI (cytochrome oxidase) fingerprint as *H. semele* over Europe. He states: 'So, if there is some genetic effect this is likely to be a very recent event probably involving a very small set of genes'.

[18] Mapping of the Orme's butterflies was finally done between 1996 and 1999 by a superb team of four research students, Matt Cowley, Jorge L. León-Cortés, David Guttiérez and Rob Wilson, working under Prof Chris D. Thomas (FRS) at Leeds University.

afield for support and failed; I still have those perfunctory letters from Ford and Cyril Clarke, who were both retiring at that stage, as I do a fading copy of the later response of Helmut Van Emden to Eric Classey when the Royal Entomological Society declined cash support for publishing the final work in January 1976. Denis Owen (who, I discovered in the New Millennium, had produced a generous review of the book)—soon to be a professor at Oxford Brookes—had not yet returned to the UK. Even so, in earnest, I set about the wider task of investigating origins over the British islands; staying in Wales became essential to finish off data gathering there: I had married Maggie in the summer of 1972; while she did her probationary teaching at Holyhead, I got on with the book under the auspices of a postgraduate training in education at Bangor (my introduction to the classroom by the Head of Geography at Friar's School was to witness, inadvertently, a boy's superb header of a globe suspended from the ceiling—a substantial depression appeared in *Heliconius* territory!).

But for the addition of a few diagrams in 1974, the book was finished by the end of August 1973,[19] when I had to return to Durham's anthropology unit. I still sit, when I can, at the distinctly 'basic' desk we bought in Bangor for shillings at which it was written 42 years ago. So what was the bottom line?—Most British butterflies had been in the UK perhaps less than 10,000 years, a number for a much shorter period, *not* 100,000 years. When regional populations dated back to earlier times (i.e., *Aricia* sibling species, as with the (now) recognised cryptic sibling *Leptidea* in Ireland), then they had evolved elsewhere in Europe or further afield. The butterflies when they came did so as an invasion, rivalling William I's land speed record for the 1066 conquest; some had no doubt done so recently, almost contemporary enough to contravene ultra-Tory immigration regulations. It was the old story: British researchers, like most Brits in every other sphere, had had too insular a focus and imagined that all was 'home made', failing to see the wider context and hotchpotch of origins.

The rest is history, as they say. The *Origins* book had raised many new issues but then left many other questions unanswered. Among the latter, some obvious ones were: Where were the European Quaternary refuges? Why are the regional changes in wing patterns so varied? How rapidly do species respond to climate change and how exactly do species with different life histories respond to climate changes? Does the McArthur–Wilson island biogeography model[20] work for butterflies on British islands (surely they are not as static as they were then held to be), and how are island faunas affected by differential species' migration capacity and colonisation potential? In fact, what resources do butterflies need to colonise a site, and just what makes up the habitat, and how do we recognise a habitat? These and many other knots were gradually unravelled over the years, thanks to research by colleagues worldwide, and different issues were taken up as different doors closed and opened on my ability to contribute to each in turn. On returning to Durham, my attention until 1978 was primarily focused on human dermatoglyphics[21]. Thereafter,

[19] Dennis 1977b.

[20] MacArthur and Wilson 1963. The seminal work on island biogeography; an elegant mathematical treatment of counter colonization and extinction rates (thus equilibrium) of species on islands.

[21] Human palm and finger prints (Dennis 1977a). See Cummins and Midlo (1961).

Fig. 18.6 The author on a field trip with boys from the Manchester Grammar School 1980

having committed a cardinal sin of turning down an anthropology lectureship at Durham and with academic posts fast dwindling in Thatcher's austerity Britain, I settled down to teaching at the school Hugh Michaelis attended in Manchester half a century earlier (Fig. 18.6); butterfly work was then a luxury left to the long summer vacations. The work on butterfly origins suggested that the focus of research should shift increasingly to contemporary issues, factors and events operating in ecological time; thus, I spent free moments in those succeeding years learning my trade in butterfly ecology and behaviour. My quarry were the most common species in Cheshire; the more conspicuous and sexually dimorphic, the easier to study (Fig. 18.7). The obvious mid-range target was a text to replace Ford's *Butterflies*. What had been achieved by one man, I gathered a team together to revise and embellish, individuals whose research is now known around the world. Inevitably, the new text was less elegant than Ford's (nothing can match it), but nevertheless it provided a mine of information for the next generation.[22] A towering pile of paper, it sat on the floor among other such examples of industry at the publisher's house awaiting funds from 1988 and was at last taken on and produced by Oxford University Press in 1992.

[22] Dennis 1992.

Fig. 18.7 Butterfly species studied in Cheshire during the 1980s. **a** Large Skipper *Ochlodes sylvanus* (female). **b** Orange-tip *Anthocharis cardamines* (male). **c** Green-veined White *Pieris napi*. **d** Common Blue *Polyommatus icarus* (male). **e** Small Tortoiseshell *Aglais urticae* (both sexes). **f** Peacock *Aglais io*. **g** Meadow Brown *Maniola jurtina* (both sexes). **h** Wall *Lasiommata megera* (male). (Courtesy of Peter B. Hardy)

But, long before this, things had changed for the worse; my time in active fieldwork came to an end soon after herniating a vertebral disc in 1983. In 1988, it was operated on; at great personal cost, I had pulled a shocked driver, as dead weight, out of his fuming car on the way back from Cambridge. Shortly after I had returned home, it was obvious that I would have to turn the job down just offered to me by Birdlife International. As a consequence, we stayed in Manchester, and I continued to work on butterflies in the vacations; from a sedentary platform, attention was switched to other issues that had arisen in the Origins, first those to do with potential changes in climate[23] (already, it was obvious from early British sources that butterfly ranges had changed markedly during the past 150 years) and then the offshore islands[24] for which only a handful of data existed in 1972–1973. In 1993, my spinal condition suddenly deteriorated—*pathemata mathemata* (παθηματα μαθηματα)—and between 1999 and 2002, a further five spinal interventions followed, the penultimate one almost fatal and caused further serious damage. The short of it is that for the past 20 years, work has had a distinctly horizontal inclination and as for mastering butterfly ecology the impression is one more of being moth-eaten. Even so, these events brought with them a mix of fortune; these calamities had happened at a convenient juncture. I had spent 15 years teaching, and the dreaded nationwide emasculation of more demanding courses (no more third year Oxbridge groups) was underway. Technology had caught up with my demands; no longer did I need to process data through the mainframe at Durham University, punch out papers on an arcane typewriter, lean over a drawing table, parcel up umpteen copies of papers for journals and subject the package to the vagaries of our flagging postal service; instead, I now had a laptop computer alongside me—loaded with new stats programmes—on the bed; I could do all the work with one hand and, then from 1996, load files quickly on the desktop and fire them off down the 'wire'. Only if instantly renovated by some extraordinary wound-healing metamorphosis would I not have registered the implications of my condition; to close down the heaped anxieties, I went at it just as hard as I could, my imagination if anything usefully enhanced by the hopelessly ineffective delicacies clinicians describe as analgesics.

A number of butterfly topics were assaulted in the new millennium. But, one final issue intrigued me more than others, especially, as during better periods, it brought me back outdoors; it arose from a haunting sentence in Ford about habitats, our inability to close in on them and yet the ability of amateurs to recognise them without being able to articulate their intuition. It comes to all of us who build a familiarity of sites and make long and careful observations. In 1996, an idea had occurred to me while dealing with British islands, and the resource-based habitat was borne. In 2002, regaining consciousness from that narrow squeak, in a morphine haze in intensive care (habitat), the idea for a paper emerged[25]: The ghostly wisps of attendants had become butterflies gliding about fuzzy blobs of equipment (resources), of which I seemed to be the key, unwilling host.

My time with butterflies began in the same year as the UK's *Butterfly Conservation;* we both started in 1968. Then, we were coming out of the historic epoch of 'dead data', the long lines of cabinet corpses (collectors' trophies), a time described so ably for the USA by William Leach in *Butterfly People*. A great deal of this collecting was pernicious; the reward was a Domesday record of life as it was and the many books describing species and their early stages. Their efforts (as others' greed) were stupendous, monumental; as they raced to collect, the very ground on

[23] Dennis 1993.

[24] Dennis and Shreeve 1996.

[25] Dennis et al. 2003.

which nature depended was being gorged on by human industry—in retrospect, the impact of collecting has been comparatively innocuous. If you do not believe me, then stand anywhere in 'England's green and pleasant land', say near the core of Derbyshire's walled-field uplands, and reflect on the sterile, nitrogen-ripened spaces that should vibrate with life;[26] so much of the UK is thus polluted, a verdant but dead zone marinated in a cocktail of chemicals. All my early observation sites on the Little Orme were soon submerged in the concrete, brick and tarmac of a housing estate: On one summer's day in the early 1990s, we drove down the new road, the once abandoned tramway between Llandudno and Colwyn Bay, where my work started and saw a fellow butterfly researcher perched on a pitiful remnant of it ineffectually releasing his Silver-studded Blues. As I write, a business park has leapt the road and is expanding, perniciously, a nondescript block of vacuous nothingness, towards the river Bollin from Manchester Airport, where in the early 1980s I studied movements of the Orange-tip.

Now, 45 years later, we are in the era of 'big data'—huge space-time data files of surveyed individuals—linked to remote satellite-harvested data, a data-gathering epidemic increasingly sweeping across swathes of the developed world, at a time when so many species are consumed by extinction. Even lepidopterists cannot escape the Dataclysm[27] but, in turn, will become easily digested data products of modern day voyeurism. We have plunged into the era of mass molecular data (which mercifully requires the collection of much smaller samples); it could also be an era of resource and life history data—'data' is the modern catchword. It is interesting how often 'data' is treated as singular as if the infinite bits of information are forgotten along with the individuals who collect them; yet, without the myriads of too often insubstantially acknowledged 'hod carriers' (recorders), the data would not exist. The pattern of papers has changed too; if you do not control, or have access to, big data and are not part of a large team (a conspiracy of arch-hod carriers), you will have to be someone very special indeed to produce a 'big' paper (not that the authors of this book have ever found that difficult). Now we are fast closing in on each species' blueprint; soon butterfly origins will be clear—Scudder would have been ecstatic and Herman Strecker apoplectic.

Ideas have been at the centre of my life; in their way, they are as beautiful and fragile as butterflies. But, on their own, and untested, ideas are comfortless creatures and need to be nurtured in a web of others, each prodded and probed in its connections, verified or rejected. I have always felt we should build up systems of tested ideas, but that is the next generation's task. No doubt it will advance much as it has always done: *Homo homini lupus*. The future of butterfly research is assured: Armies of white-coat researchers, static, incessantly and intravenously drip-fed with coffee, will be able to spend a lifetime studying them—electronic butterflies—without leaving the sanitised surfaces of a lab; they will be wired up to a Thomas J. Watson's cognitive supercomputer and be challenging orthodox theories, like dark

[26] The deeply incised Dove Valley from Hartington to Ilam, a Derbyshire 'grand' canyon, with its rich biotopes for butterflies presents an effective contrast.

[27] Rudder 2014.

matter, with lepidopteral MONDs[28] (modified Newtonian dynamics) and sesquipedalian algorithms—and will convince themselves that they understand what they study, like politicians do self-sufficiency…but may well be getting it hopelessly wrong. Why wrong? Because, little by little, they distance themselves from actually knowing butterflies in their habitats. Before you capture your butterfly, and science often requires you have to do such a thing, do spend time observing it. In these historic steps, who among researchers have been most fortunate, I ask—those, I feel (and for a moment I was so blessed), who touched the earth and felt the sun, absorbed by flickering fragility, and collapsed at a day's end satiated with living images of nature's most delicate of delights.

Acknowledgments Grateful thanks to two colleagues, Peter Hardy and the Rev. Dr Andrew Wakeham-Dawson, for their comments on the chapter and to Richard Underwood (the Raven Society) and Colin Plant (Editor of the *Entomologist's Record*) for kindly permitting photographs of Hugh Michaelis and Frank Lees to appear in these pages; Peter Hardy kindly provided the photographs of Cheshire butterflies. My grateful thanks to my gifted colleague Dr Leonardo Dapporto for his preliminary findings on the genetics of *Hipparchia semele thyone* from the Great Orme.

Dedication: *To my brother for sharing my freedom and to our mother who, in seeking hers, inadvertently gave us ours.*

References

Boyd W (1998) Armadillo. Hamish Hamilton, London
Cummins H, Midlo C (1961) Finger prints, palms and soles. Dover Publications Inc., New York
Dennis RLH (1971) The aspect of Weichselian and Flandrian geomorphological and climatic evidence in the establishment of North Wales Lepidoptera Rhopalocera. BA Dissertation, University of Durham, UK. pp 65, 12 Figs, 7 tables
Dennis RLH (1977a) A study of dermatoglyphic variation in human populations of the North Pennine Dales. PhD Thesis, University of Durham. p 741
Dennis RLH (1977b) The British butterflies. Their origin and establishment. Classey Ltd., Faringdon
Dennis RLH (ed) (1992) The ecology of butterflies in Britain. Oxford University Press, Oxford
Dennis RLH (1993) Butterflies and climate change. Manchester University Press, Manchester
Dennis RLH (2010) A Resource-based habitat view for conservation. Butterflies in the British landscape. Wiley-Blackwell, Oxford
Dennis RLH, Shreeve TG (1996) Butterflies on British and Irish Offshore Islands. Gem Publishing, Wallingford
Dennis RLH, Shreeve TG, Van Dyck H (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102:417–426
de Worms CGM Bart (1974) Frank Henry Lees (1883–1973). Entomologist's record and Journal of Variation 86:171–173
Ford EB (1945) Butterflies. Collins, London (3rd edn., 1957)
Huxley JS (1957) The three types of evolutionary process. Nature 180:454–455
Kettle DS (2000) J. W. S. Macfie M.A., D.Sc., M.B., Ch.B. Antenna 24:121–124
MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. Evolution (Lawrence, Kansas) 17:373–387

[28] Milgrom 2002.

Mattingley PF (1949) Dr J. W. S. Macfie. Entomologist 82:21–22; Carson JF (1948). Nature Lond 162:805–806. See en.wikipedia.org/wiki/John_William_Scott_Macfie
Mayr E (1963) Populations, species, and evolution: an abridgment of animal species and evolution. Harvard University Press, London
Merchant AJ (1956) *Plebejus argus* L., (Lep., Lycaenidae) *caernensis* Thompson at Llandulas and Rhyd-y-Foel. Entomologist 80:234
Milgrom M (2002) Does dark matter really exist? Sci Am 287:42–52
Pierce FN (1892) Lancashire and Cheshire Entomological Society. November 14 1892. Entomologist 3:312–313
Rudder C (2014) Dataclysm: who we are when we think no one's looking. Fourth Estate, Hammersmith

Roger L. H. Dennis is a Durham (UK) -based geographer (BA class 1, internal scholarship holder and 'one per-centre' of his year group), anthropologist (PhD and postdoctorate researcher) and butterfly biologist (DSc). As 'Doc D,' he taught geography at the Manchester Grammar School and thereafter held a number of honorary research fellowships and professorships at the Natural Environment Research Council (NERC)'s Centre for Ecology and Hydrology and several universities, the latest being The Institute for Environment, Sustainability and Regeneration (IESR) Staffordshire University. Uniquely among the authors, he is the only amateur butterfly biologist, preferring the label 'naturalist' to that of 'scientist'; his immersion in British butterfly origins occurred entirely by accident but proved an antidote to formal undergraduate coursework. Finding this medicine addictive and restorative, he went on to produce a few more publications spread across broad issues in butterfly behaviour, ecology, and biogeography; he apologizes for inflicting these on any unsuspecting readers. His last text on habitats apparently proved to be digestible to at least one reviewer, as it was awarded the 'Book of the Year' by the British Ecological Society in 2012. He attributes his idiosyncrasies, both physical and mental, not excluding his eccentric mix of predilections—classic literature, athletics, cricket, wildscape, gardens, early music and bird song, fortified wines and traditional tea rooms—to nature's botched attempt to fit a Viking frame onto a Celtic one and the random amalgam of their dissonant software.

Chapter 19
A Butterfly Has Time Enough

Robert Michael Pyle

Colorado was a stupid place to be a kid conchologist. Even so, from the age of seven, sea shells and land snails enthralled me to the point of obsession. But my passion was unrequited. I found ways to build my inland collection, but it took most of my allowance and all of my patience, neither of which was much. When I began noticing butterflies—checkered skippers buzzing over the pigweed, coppers in a marshy vacant lot—they piqued my curiosity. But it took black swallowtails gliding overhead in a ragweed canebrake, a mourning cloak sailing away above a cottonwood, and a red admiral basking in a country farmyard finally to turn my affections from mollusks to butterflies. Realizing at last that there was more satisfaction to be had as a land-locked lepidopterist, I made my first net at 11, and never looked back.

At first, books made all the difference. My father gave me Brown, Eff, and Rotger's *Colorado Butterflies* for Christmas of 1958. My mother gave me Holland's *Butterfly Book* the following Christmas. Not long after, Klots's *Peterson Field Guide* became the first book I ever bought for myself in a bookstore. The Ehrlichs' *How to Know the Butterflies* completed the initial bookshelf. These titles became my Old and New Testaments and Catechism all rolled up, completed by the classic *National Geographic* article, *Butterflies: Try and Get Them*, by Laurence Ilsley Hewes. The importance of these texts made me want to write butterfly books myself someday, a dream I little realized would be as fully satisfied as it has.

Next came my first mentors. A newspaper article led me to Ray Jae, a Denver collector and rubber worker who took me along on collecting trips into the mountains, taxing my best catches in lieu of gas money. Another amateur, Richard Buchmillar, shared techniques of spreading, dissection, and identification with me in his home lab, amidst the mingled scents of cigarillos and paradichlorobenzene. And of course, one needed a coconspirator in the hunt, as everything goes better with a pal. Happily, I was able to recruit my across-the-street best friend, Jack Jeffers, to take up netsticks with me in pursuit of the wily tortoiseshells and swallowtails.

R. M. Pyle (✉)
Founder, The Xerces Society, 369 Loop Road, Gray's River, Washington 98621, USA
e-mail: tlpyle@willapabay.org

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists*,
DOI 10.1007/978-3-319-20457-4_19

Now, when I look back on my 55 years as a lepidopterist (I joined the Lepidopterists' Society at 12), I see them as a parade of mentors, localities, incidents, and the insects themselves. Like most of us, I could write volumes about them. Many of my stories have, in fact, already been written, in books such as *The Handbook for Butterfly Watchers, Chasing Monarchs,* and *Mariposa Road: The First Butterfly Big Year*. Rather than repeat myself, I'll tell the tale through a few of the places, people, events, and creatures that have made this life possible.

First came place. I grew up in a post-war subdivision on the edge of Aurora in Denver, with not much habitat in sight. But an old irrigation ditch lined with host plants and nectar plants beneath tall plains cottonwoods ran through the hinterlands of our town. So when I finally forsook my initial passion for seashells in favor of butterflies, the High Line Canal was there to receive me, with its Weidemeyer's admirals and big chocolate wood nymphs. From age 11 to 18, I was a frequent habitué of the old ditch. My first outing took place during a spring influx of painted ladies on the dandelions, and I was a goner from then on. An annotated list of the High Line's butterflies became one of my earliest publications, and the ditch itself ran through my entire adolescence, making me who I was to become (see *The Thunder Tree*). It was also along the canal where I witnessed my first local extinctions (the Lutherans paving the parking lot where the bronze coppers once flew; my Olympia marble field becoming my junior high discus field), cementing my early passion for habitat conservation.

The High Line offered rich pickings compared to our barren neighborhood tracts. Still, a boy of the plains longed for the mountains. Fishing trips and cookouts in the Front Range helped, as did outings with Ray Jae to Deer Creek and Turkey Creek. But it was our annual trips to a family cabin in Crested Butte, in the West Elks, that made all the difference. Not only could I collect many species novel to me up there in the Gunnison Country, but those summers also led to a relationship that would change the course of my life.

One day, fishing with my dad along the East River meanders between Crested Butte and Gothic, I wandered off with my butterfly net as usual. The intoxicating perfume of mountain clover, dripping with Sonora skippers and silver-bordered fritillaries, compelled me much more than the vague promise of a small brookie on my spinning line. But this time, cresting a ridge, I looked down upon a flurry of other nets. I was astonished! I'd never encountered even one netter before, and here were what looked, to my wide eyes, like a hundred. I was terribly shy, but steeled myself to go down, introduce myself, and find out what the deal was. The nets turned out to belong to students from the Rocky Mountain Biological Laboratory (RMBL), under the tutelage of Professor Charles Remington of Yale University. I already knew that he was the cofounder of the Lepidopterists' Society, one of the Living Gods of Lepidoptera. He welcomed this dumb kid cordially and asked what I was interested in. "I love the Cer-SY'-oh-nis," I said. "Ah yes," Remington replied, "The Cer-see-OH'-nis."

For the next several summers, Remington and his RMBL colleague, Professor Paul Ehrlich of Stanford, encouraged my visits to the lab and lent enormous encouragement for my young studies, sometimes even driving me to or from Crested

Butte. On one of these trips I hiked up to Copper Lake and collected my first *Erebia magdalena,* an encounter that would greatly color my future field studies and writing life. Finally, in 1961, the annual meeting of the Lepidopterists' Society was held at Gothic; an extraordinary boon and stimulus for a boy butterfly hunter and a would-be butterfly scientist. I hung out there with the other kids: Eric Remington, Scott Ellis, and James Scott, among them. Little did I know I would one day return here as a graduate student, and eventually as a teacher myself.

Landing at the University of Washington in Seattle, I found myself in a subtle butterfly country. By virtue of that fact, no one had compiled the state's butterfly fauna since the 1940s. I lucked into fine mentors in the College of Forest Resources; Grant W. Sharpe, professor of nature interpretation, and forest entomologist Robert Gara, as well as the great coleopterist, Melville Hatch, in the last of his 50 years of teaching in zoology. Appreciating my specialist knowledge of Lepidoptera, they enabled me to write an interpretive field guide to Washington butterflies as my thesis for the Master of Science. It was later published by the Seattle Audubon Society, and became my first book, *Watching Washington Butterflies*. (Funnily enough, one of my other committee members, J. Alan Wagar, much later became president of the Washington Butterfly Association.)

These studies in turn led to a Fulbright Fellowship in England to learn about butterfly conservation at the Monks Wood Experimental Station, the only place in the world at that time where such studies were possible. My great mentor at Monks Wood was John Heath (founder of the British Butterfly Recording Scheme), and I also studied with Michael Morris, Eric Duffey, Jack Dempster, Ernie Pollard of the famous Pollard Walks, and other pioneers of insect conservation ecology. Another postgrad at Monks Wood with me at the time was Jeremy Thomas, eventually the celebrated ecologist who brought the large blue back to England, became Hope Professor of Ecology at Oxford University and an O.B.E. for his efforts.

Wondering what I was going to do with what I was learning at Monks Wood, I heard a lecture by Grahame Howarth in London one night on the impending extinction of the large blue *(Maculinea arion eutyphron)*. He said that if the large blue were to die out (as it later did), it should become a symbol so that no more British butterflies would be lost. On the train home from London that night (December 9, 1971), I realized that we had already lost the Xerces blue *(Glaucopsyche xerces)*, and that it could become such a symbol also. Thus was launched the Xerces Society. John Heath lent me all his assistance to get it going and Jo Brewer soon became my codirector. I helped to run Xerces until 1985, when the first professional staff was hired, and I have been a willing advisor ever since. When I look at Xerces' many good works today (the Society now has the largest pollinator conservation team in the world), I feel like the proud grandfather I am.

It was the founding of Xerces that drew me back to Charles Remington, who suggested that I come to the Lepidopterists' Society meeting in San Antonio in 1972 to tell about it; and then to Yale, to do a PhD with him, oriented toward butterfly conservation ecology. I did so, and returned to Gothic and RMBL in 1974 as Remington's grad student, instead of a star-struck kid. But when Alexander B. (Bill) Klots and Miriam Rothschild came to the first Xerces meeting, held at Yale in 1974, I was star-struck all over again. My eventual thesis *(The Eco-Geographical Basis for Lepidoptera Conservation)* compared Washington butterfly distribution against nature reserve coverage, an experiment in gap analysis before that field and its name had come into being. Among the great Yale collections, I indulged my special love for satyrine butterflies and drepanid moths. With Dr. Remington's strong encouragement, and the important help of Jerry Powell, Paul Opler, and Ray Stanford, Sally Hughes and I initiated the annual Fourth of July Butterfly Counts while we were at Yale in the spring of 1975.

Afterward, back in England, volunteer work for IUCN and its sister NGO, World Wildlife Fund, led to founding the Lepidoptera Specialist Group; and then to a consultancy with the Wildlife Department of Papua New Guinea (PNG). My job was to assess the embryonic Butterfly Farming and Trading Program, and to develop a conservation plan for the giant birdwings and other insect resources, which are recognized in the PNG constitution. Few postings could have been so exciting for a young naturalist as this, among Mylar-blue Ulysses swallowtails and 10-inch birdwings, my job partly to catch them and study their lifeways! Our project, under the wing of PNG-veteran Angus Hutton, inspired the butterfly farming and ranching programs that have proliferated throughout the tropical world ever since. Transferring the benefits of the insect resource from expatriate profiteers to the local populace gives them incentive to protect habitat. From PNG I went to Portland, Oregon, to serve as Northwest Land Steward for The Nature Conservancy (TNC), and did my best to infiltrate TNC with butterfly and moth culture and respect for field lepidopterists. After that I helped to set up and manage IUCN's Species Conservation Monitoring Unit in Cambridge, UK with colleague Jane Fenton, and stayed on to co-compile the first Invertebrate Red Data Book, which showed how invertebrates of every order were being affected by the same factors endangering the megafauna. I have been independent (read: poor, but free) ever since.

Even before and ever since Cambridge, for 37 years now, I have lived in an old country farmhouse in arguably the crappiest butterfly county in the USA. Wahkiakum County, Southwest Washington, boasts 130+ inches of rain per year falling on its logged-over forests, and barely 50 species of butterflies. But that fact has caused me to look around more carefully, and to value each and every butterfly I encounter. It also means there has been little lep work performed here in the past; so by default, much of what I have found here has been new, in terms of range extension, range expansion with climate change, host plants, and so on. Almost all of those years and their attendant explorations were spent with my wife Thea Linnaea Pyle, a phenomenal artist, botanist, gardener, and observer of nature, who died in 2013 (Figs. 19.1, 19.2, 19.3, and 19.4).

The depauperate nature of our local situation spurred us to range outward to find, enjoy, and study butterflies elsewhere, where they are more abundant and diverse than here. These forays have involved teaching many field seminars in butterfly ecology, including dozens for the National Wildlife and Family Nature Summits and the North Cascades and Olympics institutes; guiding butterfly collectors and watchers in many habitats tropical and temperate, including El Salvador and Guatemala with John Masters, and several times to the Mexican monarchs; following

Fig. 19.1 *Top to bottom*: *1* A Chinese hook-tip (Drepanidae), Foping National Nature Reserve, by Thea Linnaea Pyle. *2* White-lined satyr *(Lethe albolineata)* on its host bamboo, Foping National Nature Reserve, by Thea Linnaea Pyle. *3* Monarch *(Danaus plexippus)* on rabbitbrush, Dry Falls State Park, Washington, by Thea Linnaea Pyle

the migration of western monarchs for one entire autumn *(Chasing Monarchs);* and conducting the first butterfly big year *(Mariposa Road),* among many other adventures.

Most recently, Thea and I were able to investigate the butterfly fauna of some remote and wild regions of China, with Janet Chu, Paul Opler, Evi Buckner, and others, and to publish an account of the butterfly faunas and habitats of those areas. We agreed that we'd never felt so enfolded in exotic wildness, and seldom as content, as when we stood among acres of blue corydalis in the remote panda preserve known as Foping, in the Qinling Mountains. *Parnassius glacialis* and several other butterfly and moth members of its mimicry complex flew around us, and big

Fig. 19.2 Butler's alpines *(Erebia epipsodea)* and Cascade checkerspot *(Chlosyne hoffmani)* on bear scat, by Thea Linnaea Pyle

yellow-and-black skippers called *Barca bicolor* coated the streamside rocks, as giant pandas and golden pheasants roamed the bamboo forests on all sides, and giant red-and-white flying squirrels with Paul Newman-blue eyes glided like Volkswagen doors through the wild forest.

In the twenty-first century, as writing has subsumed my other professional activities more and more, butterflies have remained near the fore. My early books, including the *Audubon Field Guide to North American Butterflies,* have been followed by big books with more specific subjects: *Nabokov's Butterflies,* an extraordinary treasure-chest of the great novelists' butterfly writings; *The Butterflies of Cascadia,* a detailed field guide to the butterflies of the Pacific Northwest and its surrounding territories; and the road-trip books referred to above. If nothing else, lep studies always give a great excuse for a good road trip. But my biggest hope as an author

Fig. 19.3 *Top: 1* Pale tiger swallowtail *(Papilio eurymedon)* on lilac, Wahkiakum County, Washington, by Thea Linnaea Pyle. *2* Two-tailed tiger swallowtail *(Papilio multicaudatus),* Washington, by Thea Linnaea Pyle. *Bottom: 3* Oregon swallowtails *(Papilio machaon oregonia),* mating pair, Washington, by Thea Linnaea Pyle. *4* Anise swallowtail *(Papilio zelicaon)* on lupine, Klickitat County, Washington, by Thea Linnaea Pyle

Fig. 19.4 Luna moths *(Actias luna),* mating pair, Missouri, by Thea Linnaea Pyle

has always been that my books might be a spur and an aid to young aspirants, even as Holland, Brown, Klots, and Ehrlich inspired me. If I had any doubts of this, they were dispelled the day a boy of 11, clutching my Audubon field guide in one hand and a net in the other, met me at a Colorado nature camp. He dropped to his knees, prostrated himself, and exclaimed, “Emperor!”

Looking back, but still ahead as well because I’m not finished by a long shot, two themes seem to run through my life as refracted by butterfly scales: experience and novelty.

The experiences brought me through intimate encounters with the Lepidoptera have been as diverse as what uninitiates to the joys and trials of entomology might expect from their idea of less sedate endeavors, such as mountaineering, soldiering, or exploration. I have followed arctics and alpines to high summits under conditions that could fairly be called sublime. I have watched the largest butterfly in the world glide through the canopy of tropic forests almost gone. I have stood in a river of monarchs flowing around me in laminations of hundreds of thousands, below one of the wildest high valleys in all Mexico. And I have withstood the faerie enchantments of winged creatures that could drive a sensitive soul mad, such as Sonora blues, purple mountain emperors, and a white underwing against birchbark in a November night in the Northland.

But I have also survived the bramble patch of 16 species of thorn and briar into which I was deeply seduced on a search for the heath fritillary in gentle Devon. I came back to tell the tale of the beach-landing in a dugout in the far Louisiade Archipelago, where the native people hung back in ominous silence, poison arrows at the ready. Stung once by overcollecting Germans who had depleted their beloved birdwings, ready to take payback, they held off until we could show them the fruits of restoration on the back side of the island. And in El Salvador, temporarily abducted by the Uzi-armed militia and taken to a renegade butterfly farmer’s hideout, we emerged friends. I’ve come closer to disaster from New Mexican diamondbacks and Illinois chiggers than I have from drug-and-logging cartels in Michoacán, and

Fig. 19.5 The author and Red Cloud Mountain, San Juan Mountains, Colorado, by Scott Hoffman Black

that's pretty damn close. All for the love of butterflies! Not to mention quicksand, near-drowning, and Yukon mosquitoes.

But there have also been the novelties. I don't mean the word in the cheap sense, but in the way of things new and fresh in the world. It is not many who have the chance, in this jaded age, to participate in something that has simply not been there before. Butterflies have given me several chances to help break new ground: from the Audubon field guide to Xerces; from the first American books on butterfly watching (alongside, not instead of, collecting), to the annual butterfly counts; from following monarchs in migration and revealing some revolutionary things about them along the way, to conducting the first butterfly big year, which provided a continent-wide perspective on the current state of butterflies and their habitats.

None of these "novelties" amounted to Doing Great Science. Their delights were at least as much gifts of happenstance, grace, timing, and luck as they were initiative, and all enjoyed the help of others. They came about through being *out there, in the field,* attentive to what the insects themselves were doing, and what they had to say (Fig. 19.5). The butterflies have always been my teachers, and my inspiration. But most of all, I've had fun with butterflies. As John Steinbeck so perfectly put it

Fig. 19.6 Davin and Kristina Bagdonas, Wind River Mountains, Wyoming, by Robert Michael Pyle

in *The Log from the Sea of Cortez:* "Here was no service to science, no naming of unknown animals, but rather—we simply liked it. We liked it very much."

In these latter days, my life as a lepidopterist has taken on a new timbre and amplitude. I am devoting my present days to completing two projects, both in the works for three or four decades: the blending of natural history literature (focused on *Erebia magdalena* and its high rockslide habitat) with traditional storytelling about people, to make what I hope will be a satisfying novel; and (with Paul Hammond) a revision of the species *Lycaena mariposa* (the mariposa copper) with descriptions of several new taxa, my debut as a systematist. Meanwhile, I carry on involvement with conservation, especially for monarchs, and long-term studies of Cascadian butterfly biogeography, including climatic response. And I am still working for a federal Dark Divide Wilderness Area, special habitat for both butterflies and (maybe) Bigfoot.

If I live long enough, there are many more things I would like to do with butterflies and moths: an atlas and historical record of Lower Columbia butterflies; an analysis of *Nathalis iole* in the North, both historically and as winters warm; redoubled efforts to get insect nets back into the hands of children (Fig. 19.6), an undertaking begun as the Outernet Project of the Lepidopterists' Society; a book based around the silver satyr *(Argyrophorus argenteus)* of the Andes; and others. But if time were called tomorrow, I could not begrudge it. No matter how much time we have with butterflies and moths, it is time well spent. As the Bengali polymath Rabindranath Tagore (1861–1941, Nobel Laureate 1913) famously said,

> The butterfly counts not months but moments, and has time enough.

Perhaps that's the way it is with us: our time here is always too brief, but maybe enough, if we spend our lives largely among the butterflies.

Robert Michael Pyle is a lepidopterist, general naturalist, and writer who dwells along a tributary of the Lower Columbia River in Southwest Washington. For 35 years, he has been a professional freelance speaker, teacher, and writer of fiction, essay, and poetry. His 18 books include *Wintergreen* (winner of the John Burroughs Medal), *Where Bigfoot Walks* (subject of a Guggenheim Fellowship), *Evolution of the Genus Iris: Poems*, and a flight of butterfly books. His serial publications include many papers and notes on Lepidoptera conservation ecology and biogeography. Pyle founded the Xerces Society for Invertebrate Conservation in 1971, is a recipient of the Distinguished Service Award from the Society for Conservation Biology, and was recently appointed Honorary Fellow of the Royal Entomological Society.

Chapter 20
Butterfly Nexus

Paul R. Ehrlich

If I were young again, I'd start another butterfly collection tomorrow. Little has given me such pleasure in a long life as has science, and especially collecting butterflies and using them as tools to answer questions in evolution and ecology. And nothing has connected me to more adventures and interesting people. This was brought home to me again recently as I was going over my field notes from the summer of 1952, which I spent on Southampton Island in northern Hudson Bay working for the Canadian Defense Research Board and Department of Agriculture. I was doing biting fly surveys and general insect collecting (in those days the Reds were thought to be coming over the pole). I did the surveys, but the real reason I wanted to go to the Arctic was to study my favorite butterfly genus *Erebia*—and I owed the opportunity to a lepidopterist, Tom Freeman, head of the Northern Insect Survey. I met Tom at the first Lepidopterists' Society meeting, in New York City. I had been directed to become a charter member of that organization when I was 15 by Charles Michener, then curator of Lepidoptera at the American Museum of Natural History, and later my major professor.

Connections. Mich had conned my eager young self into mounting butterflies for him, for which he paid me by giving me dead tropical butterflies without data for my collection—and by starting me on a career in science. With Mich now 96 and me 82, we're still in touch, and a few years ago we jointly published a paper, which is now one of my favorites (Ricketts et al. 2004), with each of the four authors the major professor of the previous author!

My first summer with the Northern Insect Survey, at Hay River on the Great Slave Lake was wonderful for two of my hobbies—butterflies and flying. I got a chance to see *Erebia* in the field and to fly in a Royal Canadian Air Force (RCAF) Lancaster, the four-engined bomber that had dropped more tonnage of bombs on Germany than any other aircraft. The pilots treated me to a stall turn ("hammerhead")—exciting to say the least—and it pushed me eventually to become a multi-engine/instrument

P. R. Ehrlich (✉)
Center for Conservation Biology, Department of Biology, Stanford University, Stanford, USA
e-mail: pre@stanford.edu

University of Technology, Sydney, Australia

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4_20

Fig. 20.1 *Left:* Ikurlik, my young Inuit helper, Coral Harbour, Southampton Island, July 1952. *Right:* Location marker put on Andrews Trace, Trinidad in 1969 for *Heliconius ethilla* study with Larry Gilbert. Still there in 2004, despite vast destruction of rainforest for agriculture

pilot myself! But the second summer spent living with the Inuit (Eskimos) at Coral Harbour on Southampton Island was life-changing—even though their wife-sharing customs had pretty well been destroyed by missionaries. Learning some of a non-Indo-European language, observing the racism of the Hudson Bay company manager and of the very nice Roman Catholic Oblate missionary, Father Rio, and seeing the interactions between the Europeans and the Inuit almost set me on the path to becoming an anthropologist. Father Rio always said the Inuit were "like children," which amused me greatly when my Inuit friend Tommy Bruce regaled me with hysterical laughter about Father Rio's belief in virgin birth (Fig. 20.1).

On my way through Fort Churchill, I had been invited by botanist Dorothy Brown to join a Defense Research National Laboratory expedition at the end of the summer to Duke of York Bay at the northern tip of Southampton Island. I wanted to survey the insect fauna there, and accepted with pleasure. It turned out to be (in retrospect) the adventure of a lifetime; ice conditions and a pilot error left seven of us stranded, cold, short of food, and with polar bears around, from the 11th to the 29th of August. My most memorable day was hiking 13 miles alone (I was the only one who spoke any Inuit) to find a reported hunting camp near Cape Welsford. I located it, and got the Inuit (who hadn't seen an outsider for more than 6 months) to give us food and return the same day with me to aid our group in moving camp. We wanted to go to a place at the base of the bay where the Cleveland River's flow was keeping a stretch of water open in the bay ice, where we hoped a seaplane could get us out. It involved a lot of dog-sledding over rocks, and making a couple of Inuit friends (I introduced my wife Anne to them 34 years later).

No butterflies, and I was forced to abandon my insect collection when we were finally evacuated from a mountain lake far from our campsite. After wading miles in a partially frozen swamp to get to the mountains, we took off in an overloaded single-engine float plane (Noorduyn Norseman) from a short lake. We got back to Coral Harbour in deteriorating weather with only a few holes left in the undercast. Rather than fly out over Hudson Bay and land blind, the pilots chose to dive through a hole in the clouds, and we came out over a lake and landed. After getting to shore in a rubber raft, a freezing rain began, and we got totally lost trying to find the truck the base had sent out to pick us up; it took more than an hour to succeed. It was a harrowing rescue, but butterflies made the whole adventure possible! I recently reminisced with Dorothy Brown about it via email (which didn't exist until decades after we were stranded, and of the four other strandees I could locate, we are the last survivors).

Living with the Inuit was an unforgettable experience. In addition, I was able to officially name some geographic features visible on a globe, and that was a real thrill. But being able to observe and collect *Erebia rossii*, *Colias boothii*, *Boloria polaris*, and other Arctic butterflies, and for the first time to study birds, kept my scientific interest up, despite the paucity of women. So I determined to pursue graduate school in entomology rather than anthropology.

My first connection with butterflies came when I was introduced to collecting when I was 12 years old and in junior high school. I was soon entranced by their beauty and variety, and they channeled my desire to become a scientist (which I had strongly held as far back as I could remember). My interest led my parents to get me a copy of the first edition of W. J. Holland's *Butterfly Book* so I could identify my specimens. I still remember my disappointment when I found out that my 1898 edition had been superseded by a 1931 edition with additional plates. I soon acquired one of the latter and still have it with a plastic cover I fashioned and tabs I installed to let me move easily from group to group. I got a chance to really use that book when I was 15 and my parents let me go to a traveling summer camp in the West. One thrill then was catching my first *Parnassius* high in the Rockies. Little did I imagine that as an adult I would spend more than 50 summers doing research on Colorado butterflies based in a cabin at the Rocky Mountain Biological Laboratory (RMBL) in the West Elk Mountains. And it was more than 65 years later that I discovered, in a most interesting history book, *Butterfly People* by William Leach, that the W. J. Holland I so looked up to as a kid was a real bastard, an autocrat who treated collectors whom he hired with contempt, paid to get articles published (he had married money), and was generally a notorious opportunist.

In a way, I was following in the footsteps of nineteenth-century butterfly people, such as William Henry Edwards and Samuel Hubbard Scudder, who were champions of Darwinism and later became heroes of mine when I was a graduate student. I soon purchased used copies of Theodosius Dobzhansky's *Genetics and the Origin of Species* and Ernst Mayr's *Systematics and the Origin of Species* and devoured them. Little did I imagine then that both authors would become colleagues and family friends. Dodec reviewed my first evolution book manuscript for me and taught our daughter Lisa to ride horses at the Southwest Research Station. Ernst and I had a more than 40-year-long friendly debate about details of systematics and evolution. We remained friends even though the first time Anne and I entertained him (after I invited him to a seminar at Stanford), our cheap imitation-Swedish chair disintegrated under him just as I was making a point, depositing him in a heap of debris on our living room floor. Ernst was deeply concerned about the population explosion and often wrote me about *The Population Bomb* after I published it. When he was approaching 100, he drove into Boston to have lunch with me at Harvard for a discussion of species definitions. One of my most treasured possessions is a copy of his classic book with a beautiful inscription.

College only stimulated my interest in butterflies. With my friend Nick Gillham, I had been naming butterfly subspecies—including one after the famous collector Otto Buchholz, who had befriended us and was perhaps the first collector ever to drive West by car to hunt butterflies (in 1907). Naming subspecies is a scientifically nearly useless exercise, as a paper by Nick following one by Ed Wilson and the late Bill Brown (Gillham 1965, Wilson and Brown 1953) convinced me, but it was great fun (Ehrlich and Gillham 1951). My collection grew throughout junior high, high school, and college. It started with world butterflies and moths (much boosted by Mich's donations). In junior high, my mother used to pick me up by car whenever a cocoon I had collected in the woods yielded a big, gorgeous saturniid moth—usually a promethea or cecropia. Then I could kill and mount it for my collection, while it was still in perfect condition. Sadly, these and many other beautiful moths of the eastern USA that I enjoyed hunting are disappearing—apparently from a combination of factors ranging from street lights that attract them and habitat destruction to pesticides and parasites. My very first paper in 1948 reported that a tachinid parasitoid, *Compsilura concinnata* was attacking monarch butterflies. I did not know at the time that the fly had been imported from Europe in an attempt to control plagues of European gypsy and brown-tail moths. Ironically, that fly has been one of the prime suspects in the decline of the moths I loved.

One of the advantages for me of joining the Lepidopterists' Society was getting addresses of other butterfly collectors with whom I could exchange specimens. My very first was with a kindly Californian, Bill Hammer, who sent (I think because he realized I was a beginner) a nice collection of California butterflies in return for some very common eastern species. I'll never forget the smell of paradichlorobenzene (PDB) as I emptied the container, starting with a cascade of triangular envelopes labeled "*Euphydryas editha bayensis*." Little did I imagine that a dozen years later, I would start to develop that Bay checkerspot and its relatives into an experimental system that would occupy my attention and that of treasured colleagues for more than half a century. I've worked on it to this very day, over much of the USA and even on the other side of the Atlantic, where my friend of metapopulation fame, Ilkka Hanski, and his colleagues took up checkerspots as an experimental system (Ehrlich and Hanski 2004).

I did my undergraduate work in the zoology department of the University of Pennsylvania, where Rudolf Schmieder taught. He was the editor of *The Entomological News,* encouraged my interest in butterflies, and helped me to persuade botanist John M. Fogg, Jr., vice provost of the university, to let me leave Penn early 2 years in a row for my Arctic adventures. James A. G. Rehn, an Orthopterist, also welcomed me at the Academy of Natural Sciences of Philadelphia as a volunteer curator of butterflies (where I briefly met a young Ruth Patrick, who I knew many decades later as a dynamic scientist in her 80s and 90s). Philadelphia also served me well, since late in 1952 the Entomological Society of America was meeting there. I was anxious to go to graduate school in the fall of 1953 and had been told that Charles Michener was the best scientist working with insects. Mich had moved from the American Museum to become chair of the Department of Entomology of the University of Kansas, and that's where I wanted to go. I managed to run him down at the meeting, and miraculously he remembered me. I explained that although a wild undergrad career had resulted in lousy grades, I had published a few papers and gave him reprints. I asked Mich to give me a chance in grad school. He did more than that—he got me an assistantship with the late Robert Sokal, then a "young Turk" working on the evolution of dichlorodiphenyltrichloroethane (DDT) resistance in fruit flies.

So it was off to the wilds of Lawrence, Kansas. It was a cultural shock. Shortly after I arrived, Mich invited me to the fall entomology department picnic and I turned out to be the only man who brought a date, not a wife (I'd never heard of a picnic without girls). Amazingly, the only beverage available was Kool-Aid, so my date and I were stone-cold sober when the whole group gathered around a 50-gallon drum in which paper napkins and cups and hotdog sleeves were being burned. We were led by an old man (doubtless younger than I am now) in singing "Old MacDonald Had a Farm" (no kidding). At around the second "moo-moo here, moo-moo there," I asked my date "Who is that xxxxxxx?" using the 7-letter bad word that means "climate denier." Unluckily, Mich was standing right behind me, and he replied, "He's the dean of the graduate school." I figured I'd had a very short grad career; it was several months before I discovered that Mich's opinion of the dean was precisely the same. Unfortunately, butterflies have never been able to teach me to keep my big mouth shut.

Kansas may have been a cultural backwater in the 1950s, but the department was cutting edge. The influence of Mich and Bob Sokal on my thinking was immense; one could not ask for more challenging and thoughtful mentors. Both were brilliant. Mich was (and is still) the world's expert on bee systematics and behavior, but had also worked on butterflies. Bob, who brought statistics into biology, early on showed me how to do modern analyses of geographic variation in *Erebia*. Mich encouraged me to do my doctoral dissertation on the morphology and higher classification of the butterflies, and as I progressed, I was convinced that I was unravelling their phylogeny.

One day in a small seminar, Bob said I wasn't doing that at all, I was just grouping them together according to their overall similarities. "I could do basically the same job with correlation coefficients." Mich and three students, me, my old friend from the Arctic, Jim Chilcott, and Earl Cross (the latter two, sadly, both long gone) objected strenuously, and a couple of weeks of argument followed. Finally, Mich and Bob decided to put it to a test. Mich, then as today the world expert on bees, had a student measure 122 characteristics on 97 bee species and gave the numbers to Bob, who didn't know a bee from a beaver. A few weeks later, Bob returned with a bee "phylogeny" that Mich agreed was better than his first attempt at it (Bob accurately placed a couple of parasitic bees that Mich had originally misplaced). Thus, numerical taxonomy was born, and I was shown that a deeply held scientific belief could be dead wrong (Michener and Sokal 1957). I have never "believed" like that again.

But Mich's (and butterflies') influence on my life and happiness was even greater than that. After a few months at Kansas, I spotted, in the student union, the most beautiful woman I had ever seen. We had our first meeting in a bridge game, and discovered a mutual interest in war history in a discussion of the battle of Dunkirk. I wrote to her just before leaving on a fabulous field trip to Mexico with Mich in the summer of 1954. That provided my first acquaintance with the tropical butterflies that I would work on later for six decades (most recently in 2013 near Zihuatanejo). Anne and I corresponded during the summer, had our first date in September, and before Christmas, Anne Howland became Anne Ehrlich (interestingly, Mich had a similarly abbreviated courtship of his wife Mary).

Anne was a French and previous art major, and quickly became embroiled with butterflies. We have now worked together for 60 years, starting with her dissecting butterflies and following the footsteps of Samuel Hubbard Scudder in drawing their anatomy. Here, as in studies of ecology and evolution, butterflies turned out to be an ideal experimental system for examining the very bases of taxonomy, which until then (as I realized as a result of Michener and Sokal's pioneering work) had almost been more of an art than a science.

Anne continued to work on systematic issues and reproductive biology, doing such things as dissecting and drawing the musculature of the prothorax of even tiny lycaenids and counting eggs and spermatophores, giving us eventually an excuse to travel around the world working on aspects of butterfly anatomy and reproductive structures not possible with only preserved specimens. Later, of course, she became famous for her work on problems of population, environment, and nuclear war, all of which got her elected to the American Academy of Arts and Sciences. Sex and butterflies started it all.

When we were in Lawrence, the restaurants and swimming pool were segregated, and even the chair of the zoology department was a racist jerk named E. Raymond Hall (Hall 1946). (Full disclosure: he tried to get me thrown out of grad school for sassing him, but Mich would have none of it). My liberal parents and recent research on butterflies and subspecies had convinced me that racial classification was ridiculous scientifically and evil socially. My disgust at racism shifted to action when a distinguished Jamaican visitor arrived enraged one Monday morning at the parasitology lab of my friend Ralph Barr. He had arrived Friday afternoon and been admitted to the local hotel, but no restaurant would serve him. He fed himself for the weekend with chocolate bars from vending machines. In response, Ralph and I organized lunchtime sit-ins in Lawrence's restaurants, where a mixed group of black and white students would occupy the restaurant but would not be served. We called them "profitless lunch days." Eventually, after a bunch of adventures, the restaurants gave in.[1]

[1] It was a few years after we left Lawrence, however, before the Lawrence swimming pool was desegregated. Interestingly, when I tried to find newspaper accounts to fill in details, none could be uncovered despite the help of Kansas historian Katie Armitage and a university librarian, Barry Bunch. One theory is that by that time Lawrence, as a university town, was so ashamed of itself that the paper didn't want to carry the news. My mistake was to wait too long—those I knew who

It wasn't just my love of Lepidoptera that got Anne and me to write and illustrate our book *How to Know the Butterflies*—it was poverty. I had made the major mistake of not acquiring a rich spouse, and Anne had done the same. As a postdoc with Joe Camin, who introduced me to the ecology and evolution of mites, we were flat broke, first at the Chicago Academy of Sciences and then back at Kansas. Anne and I looked to the possibility of royalties to keep daughter Lisa, who followed quickly after our marriage, fed. We took advantage of the need for a scientifically modern, inexpensive guide to North American butterflies. Anne met our challenge by doing beautiful pen-and-ink drawings for the book. It eased our financial plight a little, and got us into a book-writing mode.

The book also produced one of the most pleasing incidents in my career. Noel McFarland, then a young moth specialist, brought me a beautiful hairstreak specimen from the Sandia Mountains of New Mexico. Although I was in the midst of writing keys to all the North American butterflies for our book, I couldn't identify the specimen to genus! In a quick field trip, I was able to find a population following Noel's directions, and by pure luck was able to work out the entire life history. With the help of a hairstreak specialist, the late Harry Clench, I named it *Sandia mcfarlandi*. It was the most distinct new butterfly species found in North America in the twentieth century—deserving of a new generic or subgeneric name (depending on your taste!).

Besides such fun, butterflies—with a little help from some water snakes—(Camin and Ehrlich 1958) got me a job as an evolutionist at Stanford University. Leaving the dismal East for the paradise of Palo Alto was, after marrying Anne, the luckiest move of my life. It also introduced me to my third great love, wine. But we ended up further financially stressed when we moved to the relatively expensive Bay Area. When I complained about my low salary, Victor Twitty, my first department chairman at Stanford, explained my situation to me. "You went into the wrong field; I promise you Stanford will never pay you a decent wage, and you must find, like most of our faculty, a way to supplement your income." That led us further into the book-writing business. Butterflies started it, and Anne drew butterflies (and other things) for Dick Holm's and my *The Process of Evolution*. Stanford has kept Vic's promise, but otherwise it has been wonderful being on the faculty of what has become the best university in the world, and especially good for a conservation biologist with broad interests. Butterflies got me to the land of milk and honey, but it was a butterfly-triggered mistake that long prevented me from getting a decent salary by the usual academic route—threatening to accept a job offer at another university and leave. Once I was lunching with Stanford's then provost, Bill Miller, and I asked him why he was keeping my salary insultingly low. "That's easy," Bill said, "we know you'll never leave Jasper Ridge."

I first heard of Jasper Ridge just after I arrived at Stanford. I attended a meeting of the West Coast Lepidopterists' Society in Santa Barbara in the early fall of 1959, driving down with a butterfly collector, Elton Sette, professionally a fisheries

had been directly involved had passed on. But again, except for butterflies I certainly would never have wound up in Lawrence or with Anne.

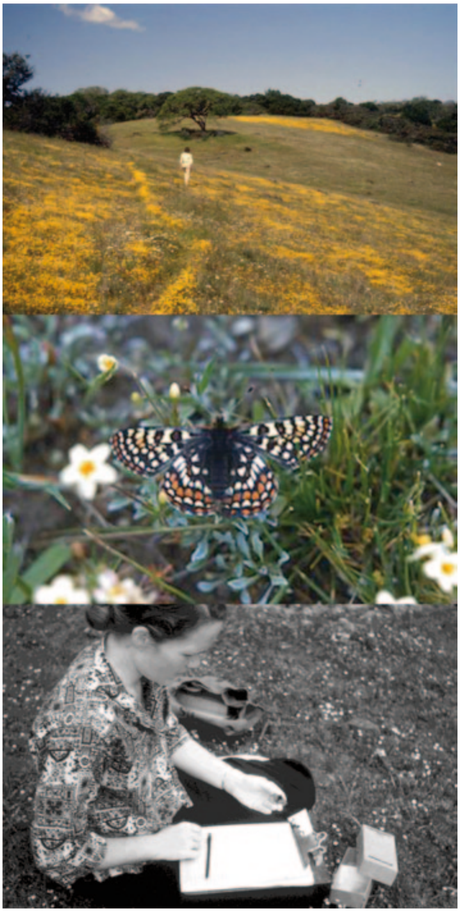


Fig. 20.2 Top to bottom: (1) Jasper Ridge Area H. Note diverse topography, which produced a series of different microclimates and allowed *Euphydryas editha* to persist longer in the face of climate change than other areas (Photo by Paul R. Ehrlich). (2) *E. editha* female on Jasper Ridge in 1960, the first year of a study that went on for more than 40 years (Photo by Paul R. Ehrlich). (3) Sue Davidson Thomas releasing a marked *E. editha* at Jasper Ridge in 1960. Sue married my late good friend and colleague, Stanford botanist John Thomas, and Anne and I still see her frequently. (Photo by Paul R. Ehrlich)

biologist who was stationed at Stanford. I told him I was looking for a butterfly population to use as a system for looking at questions in ecology and evolutionary biology. Elton told me that there was a population of *Euphydryas editha* on Jasper Ridge, an undeveloped part of Stanford's large campus (Fig. 20.2). So I was reunited with the butterfly Bill Hammer had introduced me to more than a decade earlier. I immediately visited the site, mapped it, and divided it into study areas on the map. Then on a beautiful sunny morning, March 31, 1960, at 10 a.m., I caught my first *E. editha*, a freshly-emerged male in area G, and marked it #1 with a Magic Marker (the grandmother of all felt-tipped pens). I marked another male and a female, and recaptured #1 at 11:10 about 25 ft from where it had been released. I still have that data sheet. Thanks in part to climate disruption, the species is now extinct on Jasper Ridge and in many other previous localities, but they and their relatives still exist in scattered colonies over North America, still a subject of study by me, many of my former students, and others.

Much of my fun time in the field with *Euphdryas* away from Jasper Ridge (which has become the best on-campus reserve at any major university) has been at RMBL in Colorado. It is in the wettest part of the state and provides access to habitats from 7000 to 13,000 ft elevation. RMBL is a butterfly paradise, to which I was originally introduced by Charlie Remington (he invited me and evolutionist Dick Lewontin to teach a course in biometry there in 1960, and with two exceptions I've worked there every summer since). My current research there is helping Carol Boggs and her gang on a project that my student Cheri Holdren and I started at RMBL in 1977. Carol, now a distinguished professor and director, School of the Earth, Ocean and Environment at the University of South Carolina, is married to my second longest-suffering butterfly friend (after Mich), Ward Watt. Ward was a pioneer molecular geneticist and has used *Colias* butterflies at RMBL as an experimental system for many decades. We met when I was an assistant professor and he was in high school.

Cheri was and is the wife of my close friend and colleague John Holdren, now President Obama's science advisor. He taught an environmental policy course at the lab, and Cheri and I were trying to see if what appeared to be good habitat in Colorado for *Euphydryas gillettii*, a denizen of the Rockies north of the Red Desert gap in Wyoming, actually consisted of an empty niche for that species. With permission from the lab, Cheri and I transplanted dozens of *E. gillettii* larvae from Wyoming to the RMBL area, but to make a long story short, 37 years later it is still not clear whether the transplant will "take" permanently, although barring the effects of climate disruption, the prospects look pretty good. The RMBL transplant populations have fluctuated greatly in size and have spread somewhat. The largest population established by spreading from the original transplant site was undetected for a substantial time until my colleague Chris Turnbull, visiting RMBL for the first time in several years, discovered it. She demonstrated that my regular search periphery, looking for spread of the transplants, had been too limited. The edge of the new population was just a couple hundred meters beyond where my standard search ended. Butterflies teach you to live and learn.

For all the fun I've had in North America, butterflies have actually taken me all over the world. During 1965–1966, Anne and I spent a wonderful sabbatical year in Sydney, Australia with Charles Birch, then with Charles Elton in England, and H. G. "Andy" Andrewartha in Adelaide, the world's foremost ecologist. Charles Birch and I published papers together and became fast friends, exchanging visits virtually every year until he died tragically in 2009. We still return to Oz at least once a year to see old friends.

On our 1965–1966 hegira, I got to exercise a brand-new pilot's license in Australia (Anne had just started on hers), taking collecting trips in a Cessna 172, good old VH-DIR. It took Anne and me to Gladstone to collect and dissect *Cressida cressida*, the weird papilionid that has a *Parnassius*–like sphragis. A sphragis is a prominent plug which a male makes to block a female's vagina, protecting his genetic investment in the large sperm-bearing mass (spermatophore) he has just inserted in the process of an hour or so of copulation (lucky butterflies!). It turns out that male *Euphydryas*, as my student Pat Labine showed, also plug (Labine 1964).

In some clever experiments she showed that if she re-virginized a female (removed the plug), the sperm from a second copulation were virtually the only ones that fertilized the eggs. Human males tend to be more subtle in protecting their genetic "investment." The human penis is shaped to excavate sperm from previous matings during copulation, and the last part of the ejaculate tends to be spermicidal.

While in Australia, Anne, Lisa, and I had a wonderful research trip through New Guinea and the Solomons, ending up in Guadalcanal where my butterflies brought me together with a long-time interest in war history (which I share with my colleagues Jared Diamond and Peter Vitousek). It was a real thrill to collect birdwing butterflies for dissection along the Tenaru River, site of a bloody battle between the Marines and Imperial Japanese infantry in August of 1942. I captured one specimen just a few yards from a still-live 5-inch naval round lying in a farmer's pigpen near the river.

On the way back from Oz, Anne, Lisa, and I collected and dissected through Malaysia, India (where we had the experience described at the start of *The Population Bomb*), Kashmir, and East Africa. In Malaysia, by pure chance, we ended up staying in a hotel owned by a Chinese millionaire who was deeply interested in butterflies. Anne and I showed him how to dissect and identify them. In return, he got a group of Malay aborigines in his employ to climb tall trees and snare the nearly-impossible-to-get-from-the-ground females of *Troides brookiana*, the gloriously beautiful Rajah Brooks' birdwing, for us to dissect. He also later took us on a tour of Malaysian hotels run by his Chinese friends, and treated us to the best Chinese food we've ever eaten—much to the dismay of Lisa, our then 10-year-old daughter who on that trip was always in search of hot dogs and bologna. Now she makes dim-sum herself! We also got some splendid carvings from his aborigines, and they remind us daily of Rajah Brooks. In Malawi, we met up and went on safari with my former student Michael Soule and his wife Jan. In Rhodesia, we all committed the capital crime of criticizing Ian Smith's government, but because of our skin color we were not prosecuted and did not end up on death row as did others. Michael did research on butterflies and has gone on to be a hero of the conservation movement, especially promoting re-wilding.

Soon after our return from that wonderful sabbatical, I happened to say to Peter Raven that I couldn't understand why *E. editha* larvae fed on both Plantaginaceae and Scrophulariaceae. He replied that plantagos were "just wind-pollinated scrophs," and that started discussions and investigations that led to the field of coevolution. Butterflies and plants were in a "war": plants evolving chemical defenses against butterflies and other herbivorous insects, and the latter finding ways to penetrate those poisonous barriers (Ehrlich and Raven 1964). It was a tribute to butterflies and butterfly people, who had studied their life histories so energetically and made butterflies the only large group of herbivores in which the diets of a substantial proportion of the species was known (Fig. 20.3). Much of the work on determining caterpillar food plants was done to get perfect, unworn specimens for collections—the butterfly-beauty connection that attracted me and so many others to these insects.

Fig. 20.3 *Top* to *bottom*: (1) *Opsiphanes cassia*. (2) *Anartia fatima*. (3) *Anartia jatrophae* (Photos by Paul R. Ehrlich)

Some of my most wonderful times with butterflies followed this. One piece of good luck led to powerful support of coevolution theory. Botanists had claimed that the poisons that are common in plants (and that we use as medicines, spices, recreational drugs, etc.) were actually "excretory" products. (They never explained why natural selection promoted the manufacture of energy-rich excretory compounds in plants that then didn't excrete them).

They also claimed that the "world is green" and that herbivore damage is generally trivial. By pure luck, one day at RMBL, I noticed that a small lycaenid (blue butterfly) *Glaucopsyche lygdamus* was laying eggs on the flowers of lupine plants. I recruited my botanical colleague Dennis Breedlove, and we started an experiment. We marked 100 flowering stalks of the lupines, and then carefully removed the lycaenid eggs from every other stalk. Then we recorded the seed set of each stalk. We found that the tiny butterfly actually had a gigantic impact on the plants, destroying a substantial percent of their reproductive potential, and indicating a strong selection pressure.

Field trips to Central America with students Larry Gilbert and Michael Singer, who had done pioneering work on *E. editha*, yielded many memorable times crawling with headlamps on forest floors, expecting to meet bushmasters that would strike us between the eyes, but finding *Euptychia* (=*Cissia*, a large complex of satyrine butterflies) caterpillars. A highlight was at Barro Colorado Island in Panama, where in a continuous downpour we found and photographed *Euptychia westwoodi* ovipositing on a lycopsid, one of the very few examples of a butterfly caterpillar feeding on a non-seed plant (Singer et al. 1971).

In Trinidad, Larry and I did research on the population dynamics and structure of the longwing *Heliconius ethilla*. Our results contrasted greatly with what we were finding on Jasper Ridge with *E. editha*. Females of the latter emerged with almost all their eggs—many hundreds—mature and ready to be fertilized and laid. But being a caterpillar is a dangerous thing in the tropics, where leaves are constantly patrolled by voracious ants. Larry and I found that female *Heliconius* emerged with only a handful of eggs ready to lay, gradually maturing and laying more over many weeks. The *Euphydryas* lived something like 10 days on average as adults, which, like most insects, never coexisted with adult offspring. The *Heliconius* lived up to 6 months and sometimes flew with their grandchildren.

Larry made the important discovery that female *Heliconius* actually collected pollen from certain key plants, producing clumps of pollen on their "tongues." They then secreted digestive enzymes into the clumps and sucked up the resulting amino acids. This provided them with the proteins they needed to continue egg production through their long adult lives. I had seen the special structures on *Heliconius* tongues that allow them to collect pollen but had totally missed their significance (Fig. 20.4).

Mike started a career focused on the foodplant relationships of butterflies, showed my original picture of them was dead wrong, and continues his research on checkerspots to this day as the world's expert on diet choice in herbivorous insects. Larry and Mike were great examples of a huge benefit I have enjoyed at Stanford, access to brilliant grad students from whom one can steal both ideas and credit. What more could an academic want?

Around that time, the Human Biology program at Stanford (which David Hamburg and I had co-founded) made an arrangement with Jane Goodall to, among other things, get Stanford students and faculty to do research at the Gombe

Fig. 20.4 *Heliconius erato*, collecting pollen as Larry Gilbert discovered. They secrete fluids to digest the pollen on their tongue and suck up the amino acids to support their egg production (Photos by Paul R. Ehrlich)

Stream Research Center, which she had established at the site of her chimpanzee investigations in Tanzania. Working around the chimps was always fascinating and led to some interesting adventures. At Gombe, Anne and I started a project looking at the joint dynamics of the members of a butterfly mimicry complex. At the very start, I made one of those lucky butterfly observations (along with others made of birds, reef fishes, and many other organisms in the field) that often lead to new insights. A small blue *Zizula hylax* was common along the stream where we were working. It has unusually elongate wings, and as a pilot I assumed that high aspect ratio was related to its flight behavior. But its flight was weak and it didn't glide much. Then, to my surprise, I noticed it visiting flowers of a common *Asystasia*, bloom with a deep corolla. The butterflies were crawling inside to get nectar, and, folded, their wings just fit. Evolution in action once again!

Sadly, our butterfly studies and chimp adventures at Gombe ended in 1975 when Congolese rebels under Laurent Kabila kidnapped three Stanford students and a Dutch colleague. Fortunately for us, Anne and I were not there then. It was a hideous long time for the students, who were beaten at the start and were threatened with death for months. It was heartrending for their families and the faculty of the Human Biology program. Eventually, a group of us, led by a wealthy parent, paid a ransom of $460,000 and the students were released alive. Kabila became president of the Democratic Republic of the Congo in 1997, remained corrupt and self-seeking, and was assassinated in 2001. Those he kidnapped at Gombe are all going strong.

Luck played a huge role a decade later when Anne and I were at Iguacu Falls in Brazil. There, a variety of butterflies were "mud-puddling" near a trail on earth moistened by spray from the falls. Big lizards were attacking them and gave us an opportunity to do the first systematic studies of predation on butterflies in the field, which included hints of the protective value of distastefulness in species that serve as mimicry models (Ehrlich and Ehrlich 1982). We managed some 5 hours of observations on two consecutive days, the second ending only when a group of teenagers saw what we were doing and started throwing rocks at the lizards. Sadly, I'd left my Schmeisser at home.

By that time, I'd had a transformative experience thanks to our friend Jared Diamond. We had been visiting him in his home near the University of California, Los Angeles (UCLA), and I was describing how my research group was studying the distribution of birds in montane "islands" in the Great Basin. I complained that I would like to participate, but couldn't because of my color blindness. It hadn't been a problem with the depauperate bird community in the Arctic, but I didn't think I'd be very good at censusing them in forest or brushland. Jared said that was nonsense, threw me a pair of binoculars, and took me out in his backyard. Within a few minutes, I saw a Bewick's wren and a phainopepla, and I was re-hooked on birds. Today, more than 4300 "twitches" and a lot of research later, I'm still at it, and even did more than 60 days of bird censusing in Costa Rica in the course of helping my student Gretchen Daily. For one who loves nature, birds make a great supplement to butterflies—one can go out and enjoy them on a cold spring dawn before giving a seminar at an East Coast university.

In Costa Rica, based at the Wilson Botanical Gardens, our group's favorite spot for tropical work, a butterfly research program shotgunned by Gretchen Daily was especially fun. Gretchen had started working as a student with butterfly population structure and community relations at RMBL, where we got lots of exercise dashing across fields with nets. In Costa Rica, we were more relaxed and used butterfly traps to help us understand how butterflies utilized a mixed agricultural landscape—some of the first work in "countryside biogeography," a new field that Gretchen has pioneered. I got a thrill that reminded me of "sugaring" for moths when we used bait of rotten bananas, molasses, and rum to trap gorgeous morphos, caligos, and charaxines in rainforest patches. In the course of that work, which also involved a lot of slogging through hot pastures often with wall-to-wall cowpads (a professional hazard), we realized that to get a complete picture we'd need to look at the distributions of other kinds of organisms. That led to a lot of further fun with moths (Daily and Ehrlich 1996), birds, mammals, herptiles, and even plants!

Of course, there have been downsides too. Malaria in New Guinea, a disaster in the Ngorongoro Crater, the tragic death of our friend of many adventures, Steve Schneider. Butterflies also led me into concern with human population and the environment. As a teenager, I found it very difficult to raise butterflies in northern New Jersey because so much DDT had been broadcast sprayed to kill mosquitoes. In addition, I found my collecting grounds disappearing under new housing developments. To collect butterflies, I visited my aunt and uncle who lived in Bethesda, MD, and well remember catching a Baltimore checkerspot *(Euphydryas phaeton)* in a damp field across from their house. There was a single house next door to theirs in 1946; today our daughter lives in Bethesda, it is solid house, and the checkerspots (and most other butterflies) are long gone. Overpopulation and overdevelopment were common topics of discussion when I was an undergrad at Penn, going through with the last of the World War II veterans. They laughed me out of my desire to join a fraternity, and we discussed such books as Fairfield Osborne's *Plundered Planet* and Bill Vogt's *Road to Survival*.

The trend of habitat destruction has followed me throughout my career. Almost everywhere I have worked with butterflies, Panama, Gombe, the San Francisco Bay Area, Colorado, Spain, New Guinea, Mexico, Malaysia, Costa Rica, New Jersey, Bethesda, you name it, and I've seen natural areas in retreat before an expanding human enterprise. The increasingly depauperate lepidopteran fauna of the eastern USA and the Bay Area always makes me wish they could be restored to their previous glory. The famous lepidopterist, William Henry Edwards wrote of seeing "countless" zebra swallowtails *(Graphium marcellus)* in West Virginia in the 1860s. I still remember with a thrill catching the only one I have ever seen, in a glen along the Chesapeake and Ohio (C&O) canal near Washington, DC 80 years later. My friend Dennis Murphy seems to share a special curse—once in Colorado and once in Nevada, we went together to sample known checkerspot populations and found on arrival bare ground rich in sheep or goat droppings, and no sign of butterflies or their food plants. Almost as bad, when we were trying to sample a California population near the Mexican border, I was bitten by a drug smuggler's dog and had to get treated to ward off possible rabies. But worst of all was as Dennis, I, and others slowly realized that the 1200 acre reserve of Jasper Ridge was inadequate to support even one population of a small herbivorous insect, and watching *E. editha* go extinct there partly in response to climate change that made all of its small habitat useless or marginal.

Despite such adventures and downers, butterflies, as I have said, brought me enormous joy and incredible opportunities to "see the world." But in letting me see, as Aldo Leopold called it, that "world of wounds," butterflies have also produced in me a deep sadness—and a drive to reverse the ongoing destruction of the living world before it's too late (Ehrlich and Ehrlich 2013). But even in the sad domain of conservation, in the face of constant failure, being able to work with an incredible group of colleagues and good friends to avoid collapse has kept my butterfly-generated luck intact. I wish the butterflies luck too—I'm reasonably sure *Pieris rapae* will outlast all of us.

But it has really been worth it. I can hardly begin to remember all the natural history doors butterflies have opened to me: the behavior and community ecology of butterfly fishes on Australia's Great Barrier Reefs (Ehrlich et al. 1977); synchronous fireflies on a forest trail in New Britain; a sun bittern on a mountain stream in Braulio Carrillo park in Costa Rica; a nearly all-white male Truk monarch near the lagoon that was a graveyard of Japanese ships in World War II; thousands of wildebeests swimming the Mara River in the Serengeti; a Bengal tiger and its prey in the Kanha Reserve in India; mixed species schools of grunts and goat fishes on the coral reefs of St. Croix in the Caribbean; tinamous and giant hummingbirds in the high Andes; a Ross gull on Cornwallis Island in the high Arctic; elephants playing in a river in the Okavango Delta; wading in penguin shit in Antarctica (the only butterfly-free continent); and mobs of *Papilio machaon aliaska* and *Parnassius eversmanni* seen while driving the Alaska highway.

The latter trip was with demon collectors Floyd and June Preston in the summer of 1955, while Anne stayed home pregnant with Lisa. Selling specimens later helped keep Lisa in expensive formula. The next summer, I worked on mosquitoes for the US Air Force in Alaska, got to stay in bachelor officers' quarters (BOQ) with a fighter squadron at Ladd air force base (like living with a motorcycle gang), and at Kotzebue collected *Erebia rossii kuskoquima, Erebia fasciatak avinoffi*, and *Erebia mackinleyensis*. In Alaska, I got my first chance to handle the controls of an airplane, and remember clearly my veteran bush pilot landing us on a beach ridge at Shishmaref, a ridge now gone as sea level rise is eroding away the town. And, of course, every summer included the *Erebia, Oeneis, Colias, Glaucopsyche, Papilio, Chlosyne*, and other marvels of the Copper Creek valley above RMBL. I wouldn't trade those, Anne, and the students and dear friends who have shared them with me, for anything. I have had a very lucky life.

References

Camin JH, Ehrlich PR (1958) Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie. Evolution 12:504–511

Daily GC, Ehrlich PR (1996) Nocturnality and species survival. Proc Natl Acad Sci U S A 93:11709–11712

Ehrlich PR, Ehrlich AH (1982) Lizard predation on tropical butterflies. J Lepid Soc 36:148–152

Ehrlich PR, Ehrlich AH (2013) Can a collapse of civilization be avoided? Proc R Soc B 280:20122845. http://rspb.royalsocietypublishing.org/content/280/1754/20122845

Ehrlich PR, Gillham NW (1951) A new Atrytone from Nebraska (Lepidoptera: Hesperioidea). Entomol News 62:188–189

Ehrlich PR, Hanski I (eds) (2004) On the wings of Checkerspots: a model system for population biology. Oxford University Press, Oxford

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18:586–608

Ehrlich PR, Talbot FH, Russell BC, Anderson GRV (1977) The behaviour of chaetodontid fishes with special reference to Lorenz's "poster colouration" hypothesis. J Zool Lond 183:213–228

Gillham NW (1965) Geographic variation and the subspecies concept in butterflies. Syst Zool 5:100–120

Hall ER (1946) Zoological subspecies of man at the peace table. J Mammal 27:358–364

Labine PA (1964) Population biology of the butterfly, *Euphydryas editha*. I. Barriers to multiple inseminations. Evolution 18:335–336

Michener CD, Sokal RR (1957) A quantitative approach to a problem in classification. Evolution 11:130–162

Ricketts TH, Daily GC, Ehrlich PR, Michener CD (2004) Economic value of tropical forest to coffee production. Proc Natl Acad Sci U S A 101:12579–12582

Singer MC, Ehrlich PR, Gilbert LE (1971) Butterfly feeding on Lycopsid. Science 172:1341–1342

Wilson EO, Brown WL (1953) The subspecies concept and its taxonomic application. Syst Zool 2:97–111

Prof. Dr. Paul R. Ehrlich is Bing Professor of Population Studies, president of the Center for Conservation Biology, Department of Biology, Stanford University and adjunct professor, University of Technology, Sydney. He does research in population biology (including ecology,

evolutionary biology, behavior, and human ecology and cultural evolution). Ehrlich has carried out field, laboratory, and theoretical research on a wide array of problems ranging from the dynamics and genetics of insect populations, studies of the ecological and evolutionary interactions of plants and herbivores, and the behavioral ecology of birds and reef fishes, to experimental studies of the effects of crowding on human beings and studies of cultural evolution. He is heavily involved in the Millennium Alliance for Humanity and the Biosphere (MAHB–http://mahb.stanford.edu/) and is author and coauthor of more than 1000 scientific papers and articles in the popular press and over 40 books. Ehrlich is a Fellow of the American Academy of Arts and Sciences, the American Entomological Society, and the Beijer Institute of Ecological Economics, and a member of the US National Academy of Sciences and the American Philosophical Society. He is a Foreign Member of the Royal Society, an Honorary Member of the British Ecological Society and an Honorary Fellow of the Royal Entomological Society. Among his many other honors are the Royal Swedish Academy of Sciences, Crafoord Prize in Population Biology and the Conservation of Biological Diversity (an explicit replacement for the Nobel Prize); a MacArthur Prize Fellowship; the Volvo Environment Prize; UNEP Sasakawa Environment Prize; the Heinz Award for the Environment; the Tyler Prize for Environmental Achievement; the Heineken Prize for Environmental Sciences; the Blue Planet Prize; the Eminent Ecologist award of the Ecological Society of America, the Margalef Prize in Ecology and Environmental Sciences, and the BBVA Frontiers of Knowledge Award in Ecology and Conservation Biology. Dr. Ehrlich has appeared as a guest on more than 1000 TV and radio programs; he also was a correspondent for NBC News. He has given many hundreds of public lectures in the past 50 years.

Index

L. A. Dyer, M. L. Forister (eds.), *The Lives of Lepidopterists,*
DOI 10.1007/978-3-319-20457-4

D

T

X

Y

Z